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Studies of Predators of the Balsam Woolly Aphid, *Adelges piceae* (Ratz.) (Homoptera: Adelgidae) VIII. Syrphidae (Diptera)[1,2]

By N. R. Brown[3] and R. C. Clark[4]

Several species of native syrphids have been found to prey upon the introduced balsam woolly aphid, *Adelges piceae* (Ratz.), in New Brunswick and three of these, *Syrphus torvus* O. S., *Metasyrphus lapponicus* (Zett.), and *Neocnemodon coxalis* (Curr.), are sometimes very common. As part of a long-term study of the biological control of the balsam woolly aphid by native and introduced predators, the life histories, natural control, population fluctuations and control value of these native syrphids have been investigated.

Descriptions for Field Identification

It has been necessary for the study of the predators of the balsam woolly aphid to be able to distinguish rapidly all predacious species in whatever stage they may occur on infested trees. Characteristics for field identification of some other dipterous predators (Chamaemyiidae) have been published in previous papers in this series (Brown and Clark, 1956; Clark and Brown, 1957) and have been useful not only to the writers but to other workers as well. The characters described below were those found to be most useful in the identification of most stages of the three syrphid species commonly found feeding on the balsam woolly aphid in New Brunswick.

***Syrphus torvus* O. S.**

Egg (see Fig. 1).–Length 1.35 mm. Width 0.37 mm. Greyish-white, subcylindrical, tapering slightly towards the ends with micropylar end slightly blunter. Surface dull, covered with a fine raised reticulation formed by minute elevations from the outer ends of which project from 6 to 8 fine short radiating arms; the elevations more or less arranged in a spiral (about 45°) around the egg. Deposited on trunk of infested tree, usually on exposed bark but occasionally in prey "wool" masses; probably also laid on needles.

Larva, Instar I (see Fig. 2).–Length 2-3 mm. Width 0.8 mm. Posterior respiratory processes small, brown, widely divergent, not joined at base. Colour light yellow-green. Body elongate wedge-shaped; anterior end sharply pointed; posterior end blunt; dorsum arched; venter flat. Integument smooth with segmentation distinct. One row of fairly long amber-coloured setae across each segment. General description – a small yellow-green larva with rows of long setae across the segments.

Larva, Instar II (see Fig. 3).–Length 3.63 mm. (av. 36 specimens); range 2.72-5.84 mm. Width 0.90 mm. (av. 36 specimens); range 0.64-1.60 mm. Posterior respiratory processes small, round, adjacent, brownish-yellow. Colour basically yellow, with some indication of orange or light-green; black areas of varying extent along sides of mid-dorsal line. Body subcylindrical to wedge-shaped; anterior end with long blunt taper; posterior end truncate; dorsum arched; venter flat. Integument smooth, but may be somewhat wrinkled; seg-

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[2]Joint project of Forest Biology Division, Fredericton, N.B. and Department of Lands and Mines of New Brunswick, financed in part by funds from the Provincial Department.
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mentation distinct; inconspicuous rows of setae segmentally arranged. General description – a yellowish larva with blackish areas along the mid-dorsal line.

Larva, Instar III (see Fig. 4).–Length 10-13 mm. Width 3-4 mm. Posterior respiratory processes visible from above as rather small, round globular structures, not or barely contiguous; brownish. Colour basically orange with varying amounts of wide black areas subdorsally. Body elongate wedge-shaped; anterior end with long blunt taper; posterior end truncate; dorsum arched; venter flat. Integument smooth, with some wrinkling; segmentation distinct. Segmental rows of setae short, inconspicuous. General description – orange, usually with wide blackish subdorsal markings, sometimes brightly coloured; approximately ½ inch long; posterior respiratory processes almost spherical, contiguous.

Puparium (see Fig. 5).–Length 7 mm. (av. 5 specimens); range 6.5-7.5 mm. Width 3.2 mm. (av. 5 specimens); range 3-3.5 mm. Light golden brown to dull yellowish; may have six or seven black dots in a median dorsal row; thin dark lateral line along each mid-lateral region. Tear-drop shaped, with almost circular cross-section; anterior end bluntly rounded; posterior end pointed; dorsum very strongly arched; venter slightly flattened. Integument may appear silky; segmentation indistinct. Posterior respiratory processes same as Larva III. Usually found in the forest floor; probably mostly formed in the duff layers above mineral soil. General description – large, golden-brown or yellowish, sometimes lightly marked with a row of median dorsal small black spots; posterior respiratory processes small, round.

Adult (see Fig. 6).–Length 8-10 mm. General colour black with yellow markings. Frons light yellowish with frontal tubercle of same colour; eyes contiguous in male, separated in female. Thorax light metallic greenish-blue dorsally, scutellum light flesh-coloured to yellowish. Abdomen banded yellow on black background; first transverse yellow band broken mid-dorsally into two large spots; remaining yellow bands complete. Hind femora straw-coloured with basal part black, this black extending from ¼ to ½ the length. Wings hyaline, stigma lightly clouded; 3rd vein (R_{4+5}) slightly curved into first posterior cell.

Syrphus is the only genus of the Syrphinae with long, fine hairs on the posterior part of the upper surface of the lower squama; *S. torvus* is the only species of *Syrphus* with hairy eyes – these hairs are much shorter in females than in males and are not visible using a hand lens. The presence of broken or unbroken second and third abdominal bands is not sufficient to distinguish *S. torvus* from *M. lapponicus* as both conditions occur in both genera.

***Metasyrphus lapponicus* (Zett.)**

Egg (see Fig. 7).–Length 1.25 mm. Width 0.43 mm. Milky white; elongate-oval, tapering towards both ends but with micropylar end much blunter. Surface shiny; closely covered with fine elongate markings which are more or less arranged in rows but which do not give the appearance of being raised. Deposited on bark or on needles, usually in the open.

Larva, Instar I (see Fig. 8).–See Instar III for description.

Larva, Instar II (see Fig. 9).–See Instar III for description.

Larva, Instar III (see Fig. 10).–Length 12-15 mm. Width 3-4 mm. Posterior respiratory processes short, roundish, contiguous, recessed in fleshy folds of integument and usually not visible from above; dark brown. Colour greyish with subdorsal brownish markings; six distinct short, whitish transverse markings across mid-dorsal line. Body wedge-shaped; anterior end pointed; posterior end

truncate; dorsum arched; venter flat. Integument wrinkled, granular; segmentation indistinct due to many transverse foldings. Segmentally arranged setae very short and inconspicuous; a light dusting of small pieces of *Adelges* "wool" often present. General description – robust, greyish, with six conspicuous, short transverse dorsal white markings; posterior respiratory processes hidden from above by fleshy folds of the integument; sometimes covered with a light powdery dusting of *Adelges* "wool".

All three larval instars basically alike in appearance, the greyish colouration and six transverse whitish markings being characteristic.

Puparium (see Fig. 11).–Length 6.75 mm. (av. 10 specimens); range 6.5-8 mm. Width 3.25 mm. (av. 10 specimens); range 3-4 mm. Greyish-brown with a feathering of short transverse black bars and a few roundish black spots; the transverse whitish markings of the larva are present but not as conspicuous. Elongate-oval, tapering posteriorly; cross section almost circular; anterior end bluntly rounded; posterior end tapered to a blunt point; dorsum strongly arched; venter slightly flattened. Integument smooth, but has a dull appearance; segmentation indistinct; sometimes a few pieces of *Adelges* "wool" adhering to puparium. Posterior respiratory processes small, round, contiguous, brownish-black in colour; visible from above. Usually formed adhered to open bark by posterior end, with anterior end downward; occasionally formed in more protected locations. General description – large, grey, more elongate than *S. torvus*, showing an indication of the transverse whitish larval markings; formed anterior end downward on the trunk.

Adult (see Fig. 12).–Length 10-11 mm. Black with yellow markings. Frons flesh-coloured to light yellowish; frontal tubercle clouded with black; eyes contiguous in male, separated in female. Thorax metallic bluish-black dorsally; scutellum dull flesh-coloured. Abdomen black, with first three yellow bands broken mid-dorsally into spots; 2nd and 3rd pairs of spots curved, concave anteriorly. Hind femora mostly blackish, with some straw-coloured area at apex. Wings hyaline, stigma generally darker than in *S. torvus;* 3rd vein (R_{4+5}) strongly curved into first posterior cell.

Metasyrphus has only short dense pubescence on the posterior part of the upper surface of the lower squama, but no long, fine hairs. *M. lapponicus* separates from other species of *Metasyrphus* by the following characters: (1) metasternum bare, third longitudinal vein curved into first posterior cell; (2) second and third abdominal bands broken into spots (Fluke, 1952).

***Neocnemodon coxalis* (Curr.)**

Egg.–Not observed.

Larva, Instar I.–Length 1.5 mm. Width 0.34 mm. Segmental setae prominent, almost colourless and not as long as in *S. torvus*. See Instar III for complete description.

Larva, Instar II.–Length 3.16 mm. (av. 2 specimens). Width 0.72 mm. (av. 2 specimens). See Instar III for description.

Larva, Instar III (see Fig. 16).–Length 5.83 mm. (av. 7 specimens); range 4.40-6.40 mm. Width 1.99 mm. (av. 7 specimens); range 1.52-2.32 mm. Posterior respiratory processes long (av. 0.33 mm. for 7 specimens), projecting posteriorly and slightly dorsally, not enlarged at apices, contiguous for entire length and arising from a membranous, grey, cone-shaped base; colour red-brown or brown-black. Larva uniformly grey or fairly uniformly dull reddish-brown. Shape elongate-oval; anterior end bluntly rounded to tapered; posterior end

bluntly rounded to truncate; dorsum rounded, but much flatter than *Syrphus* or *Metasyrphus;* venter flat. Integument rough, granulose; segmentation indistinct due to very extensive folding of integument. Generally bare, but occasionally has some *Adelges* "wool" adhering. General description – dull, wrinkled, uniformly grey or reddish-brown with projecting posterior respiratory processes.

All three larval instars very similar, characterized by dull greyish colour. The elongated contiguous posterior respiratory processes are characteristic of the last instar but those of the first two instars are not conspicuous.

Puparium (see Fig. 17).–Length 4.5 mm. (av. 6 specimens); range 4-5 mm. Width 1.9 mm. (av. 6 specimens); range 1.5-2 mm. In general appears blackish in colour; dorsal background colour dull blackish-orange with conspicuous row of large black spots dorso-laterally on each side and with numerous other small scattered black markings; venter dull blackish. Shape elongate-oval; cross section more or less circular; anterior end strongly rounded; posterior end tapered; dorsum strongly arched; venter flat. Integument dull, smooth; segmentation indistinct. Posterior respiratory processes long, visible from above, projecting postero-dorsally at angle of from 30° to 45°. Usually formed in protected places on the trunk, in cracks, crevices, under bark scales; very occasionally found on open bark. General description – small, dark-coloured, with black markings; posterior respiratory processes elongate, contiguous for entire length; usually formed in protected locations on the trunk.

Adult (see Fig. 18).–Length 6-7 mm. Colour black. Frons black; eyes contiguous in male, separated in female. Thorax black. Abdomen black. Legs mostly black; some yellowish-brown markings. Wings hyaline, stigma very light brownish.

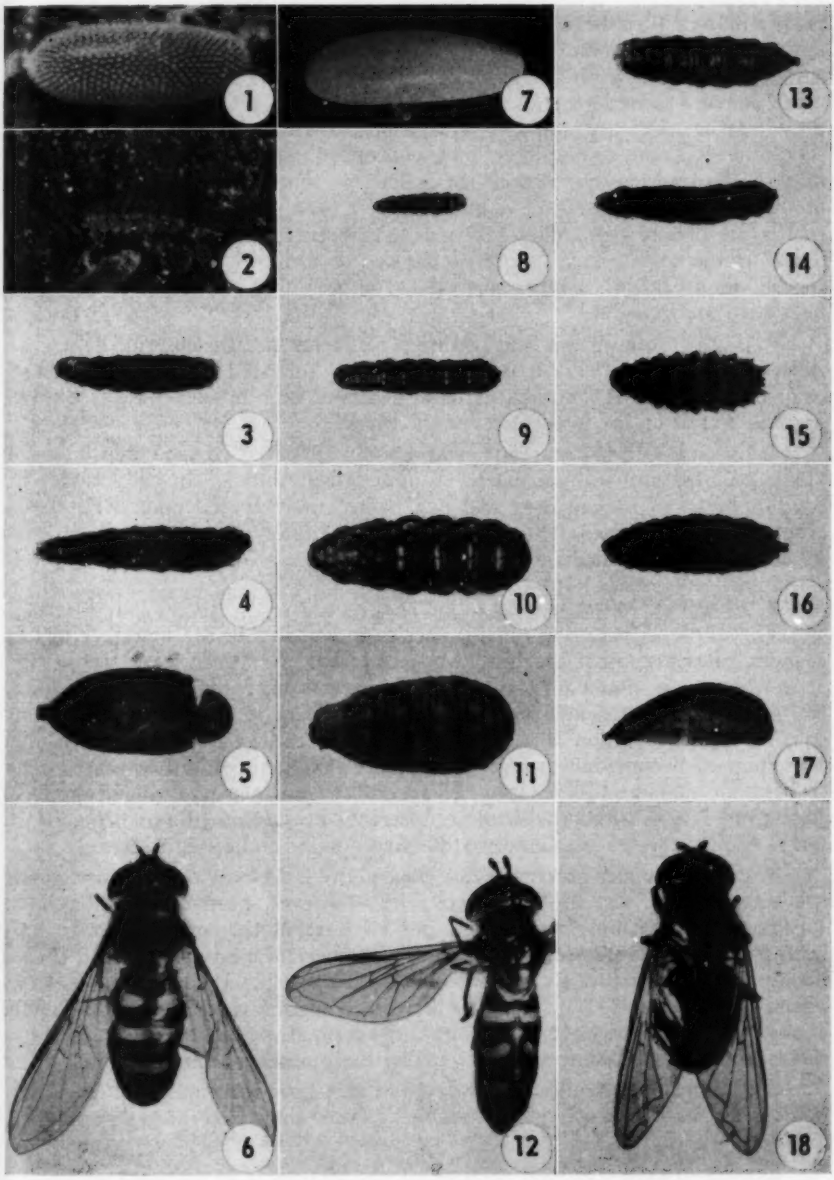
A member of a difficult group taxonomically, only the males of which can be determined with certainty.

Life History and Habits

***Syrphus torvus* O. S.**

This is a very common, widespread syrphid which has been recorded feeding on a great variety of prey species. The literature is vague concerning the number of generations per year and the exact duration of the stages. Metcalf (1911) said that the species was abundant at Columbus, Ohio and was taken from April 1 to September 10; he indicated that an autumn generation of larvae was present during the last half of September and the first half of October in one year and until at least the first of November in another year. Metcalf (1916) also reports an adult emerging on May 7 from a puparium hibernating beneath leaves. Curran (1920), who studied this and other species in southern Ontario, records it as an important species, emerging during the first warm days in spring and ovipositing among the first colonies of aphids (stem mothers) appearing on various plants. Again in the autumn he records it as preying on the return migrants and sexual females as well as feeding on summer forms of aphids on various plants. Both authors indicate that two, and possibly more than two, generations occur per year.

As a predator of *A. piceae* in New Brunswick this species occurs only in one well-defined generation, feeding in spring and early summer on the hiemosistens generation of the prey. Eggs are found from the first week in May until about June 10. First-instar larvae have been recorded from May 8 to June 1, second-instar larvae during the last half of May and the first half of June, and third-instar larvae from about May 25 to almost the end of June. Puparia have been found



Figs. 1-6. *Syrphus torvus*. 1, egg; 2, larva, instar I beside egg shell; 3, larva, instar II; 4, larva, instar III; 5, puparium; 6, adult. Figs. 7-12. *Metasyrphus lapponicus*. 7, egg; 8, larva, instar I; 9, larva, instar II; 10, larva, instar III; 11, puparium; 12, adult. Figs. 13-15. Unidentified syrphid larvae. Figs. 16-18. *Neocnemodon coxalis*. 16, larva, instar III; 17, puparium; 18, adult.

as early as May 22. Adults have emerged from field rearing cages or have been collected from June 19 to August 13, with the majority having emerged by the middle of July. Larvae have not been recorded feeding on the summer, or aestivosistens, generation of *A. piceae*. From the work of Metcalf and Curran noted above, a second generation might be expected to occur, but if this is so, the prey must be other species of aphids in the general area. It is not known why this should be so, as the aestivosistens prey generation is often much more numerous than the hiemosistens generation, particularly in recently established infestations of the type in which most of our studies have been made. In mid-September a few larvae closely resembling *S. torvus* have been found feeding on *A. piceae*. These larvae were not as brightly coloured as spring *S. torvus* larvae, having the orange areas with a more washed out appearance. Attempts to rear these have been unsuccessful.

It has been found from field rearing experiments in cages described elsewhere (Clark and Brown, 1959) that the majority of fully-fed larvae go to the soil prior to pupation. A few puparia have, however, been noted on the tree trunks near the soil or on the lower parts of the cages.

First- and second-instar larvae have been observed to feed mostly on *A. piceae* eggs but also to some extent on intermediate instars. In one instance the remains of seven sucked eggs and one being currently fed upon were found around one small larva. Third-instar larvae feed mostly on adult prey and to a lesser extent on intermediate instars and eggs.

***Metasyrphus lapponicus* (Zett.)**

Very little information on this species is available in the literature and no account of the seasonal life history was located. At Fredericton, larvae first appear about the middle of May and in some years are common until nearly the end of June. The earliest larval record in our files is May 20 and the latest date for first generation larvae is June 28. The earliest pupation date is June 2 and puparia become numerous by the middle of June. Adult emergence occurs from about June 5 to July 9, the peak period of emergence varying from about June 25 to July 6. Records show no difference in the time of emergence of the sexes. Laboratory rearing indicates the pupal period to be 5 or 6 days.

The early summer generation described above is the only one that is regularly predacious on *A. piceae*. The species has, however, been collected in much smaller numbers from *A. piceae* infestations later in the season. Larvae have been found on July 17, August 28, and September 26; an adult emerged from a field-collected puparium on July 20 and an adult was observed ovipositing on an infested twig on July 27. These latter records suggest that a few of the adults emerging in June and early July oviposit again on *A. piceae* infestations but that the majority seek other prey species among the forest aphids.

Eggs, intermediate instars, and adults of *A. piceae* form the food of *M. lapponicus* larvae, with instar preferences being very similar to those described for *S. torvus*.

Rearing in field cages has shown that the puparia of this species are formed on the trunks of infested trees, where the larvae fed. The puparia hang head downward, attached at the posterior end by a mucilaginous substance secreted by the larva. As puparia are not found on the trunks in late fall or early spring, the adults that oviposit among the hiemosistens generation of *A. piceae* must fly back to these infestations from the places where the alternate host species occurred during the previous summer. It is not known whether the species over-

winters in the ground or above ground, or whether the puparium or adult is the overwintering stage. The spring eggs are not as often laid on bare areas of bark as are those of *S. torvus* and, being laid later in the development period of the prey, are not as visible and not as often observed as are the eggs of *S. torvus*.

***Neocnemodon coxalis* (Curr.)**

No account of the seasonal life history of this species was found in the literature. As a predator of *A. piceae* two fairly well-defined generations occur per year. Third-instar larvae hibernate and most of these do not feed the following spring before pupating. Puparia are formed in the spring on the trees, usually under bark scales and in crevices and other protected places. Possibly puparia are sometimes formed in the upper layers of the forest floor. Emergence of adults of this generation occurs from April 15 to about June 8.

Larvae of the summer generation occur most commonly from mid-June to mid-July and adult emergence has been recorded from July 31 to August 29.

Larvae of the overwintering generation are generally more numerous than those of the summer generation and have been found as early as August 5. Large numbers of larvae have been recorded in some years, particularly during mid-September. Larvae can be found on the trees, feeding on *A. piceae* until the first heavy fall frosts cut off their food supply in October or November.

The larvae feed on eggs, intermediate instars, and adults of *A. piceae*.

Natural Control

Parasitism of syrphids by several species of Hymenoptera is common and undoubtedly has an important effect on the effectiveness of the predators as control agents of *A. piceae*. Although we have made no estimate of parasitism, Atwood (1933) stated that all species are heavily parasitized by an unidentified Ichneumonid and that the rate of parasitism must have been not less than 75 per cent. (The Ichneumonid was probably *Syrphoctonus*.)

Hymenoptera, Ichneumonidae

Promethes sp.—Four specimens of this undescribed species emerged singly from *N. coxalis* puparia in 1959. One emerged on May 22 from a puparium collected on May 12. Three adults emerged from June 1-8 from larvae collected early in the spring and placed in a field cage for rearing. Host larvae are apparently parasitized by this species but it is not known whether this occurs during the previous autumn or early in the spring.

Syrphoctonus agilis Cress.—This species has been recorded as a parasite on all three syrphids and is the species most commonly reared from *M. lapponicus* and *N. coxalis*. Emergence from *S. torvus* puparia occurs during mid-July. Adults emerge from *M. lapponicus* puparia throughout July but one adult emerged in rearing on June 14. Emergence from *N. coxalis* puparia has been recorded at two periods – during June and during the last half of August. These records indicate that at least two generations of *S. agilis* occur each season, using as host whatever syrphid species is available at the time. Overwintering probably occurs in the adult stage.

S. agilis parasitizes *N. coxalis* when the host is in the larval stage, as shown by recovery of the parasite from puparia obtained from field cage rearing of field-collected larvae. Although many field-collected larvae of *S. torvus* and *M. lapponicus* were reared in field cages in 1959, no *S. agilis* emerged from puparia subsequently formed from these larvae. This may possibly be explained by the fact that most of the larvae were in either the first or second instar when

caged and may indicate that parasitism occurs only when the host larva is in the third instar.

Syrphoctonus sp.—A few adults, determinable only as *Syrphoctonus* sp., have been reared from puparia of *M. lapponicus, N. coxalis,* and from unidentified syrphid puparia. Emergence dates have been: July 17 for the single specimen reared from *M. lapponicus,* May 4 and from. June 8-24 for specimens reared from *N. coxalis,* and June 4 and 30 from unidentified puparia.

Phthorima bidens (Ds.).—Only eight adults of this parasite have been recovered, all from *N. coxalis* puparia excepting one from an unidentified syrphid puparium. Some of the host puparia were field-collected and some were from field-collected larvae which formed puparia in a field rearing cage. Emergence dates were from May 25 to June 27. Adult parasites apparently oviposit in the host larva.

Hymenoptera, Encyrtidae

Syrphophagus quadrimaculatae (Ashm.).—Four groups of this multiple parasite have been reared from *N. coxalis* puparia, emerging from May 25 to August 4. Two groups emerged from field-collected puparia and two groups from puparia formed by field-collected larvae. In one case, three *Asaphes* ? sp. and four *S. quadrimaculatae* emerged from the same puparium. The maximum number obtained from a single puparium was seven. Female adults predominated in all groups. One adult has been collected in the field on an *A. piceae* infested balsam fir tree and one on a white pine tree infested with *Pineus strobi* (Htg.). The host is apparently attacked while in the larval stage.

Hymenoptera, Pteromalidae

Asaphes ? sp.—One group of three female adults of this undescribed species was obtained (July 8) from a field-collected *N. coxalis* puparium. Four *Syrphophagus quadrimaculatae* adults also emerged from the same puparium.

Pachyneuron allograptae Ashm.—Four groups of adults have been reared from *M. lapponicus* puparia and one group from a *N. coxalis* puparium. All puparia were field-collected. Adults emerged from June 21 to July 23. Emergence from single puparia was 3, 6, 11, 13 and 33 adults. Sex ratio varied in the different groups but males predominated. On June 27 a female was collected in the field on an unidentified syrphid puparium. It appears likely that puparia are parasitized by the parasite adults, as is the case with *P. altiscutum* How., a parasite of the chamaemyiid predators of *A. piceae.*

Pachyneuron sp.—One group of 14 adults emerged from a field-collected *S. torvus* puparium in July.

Euneura lachni (Ashm.).—One female adult emerged from a *N. coxalis* puparium on August 24.

Only one instance of predation on syrphid larvae has been observed. On June 29, 1956 a female ant, *Formica fusca* L., was collected while it was feeding on a syrphid larva (probably *N. coxalis*).

Population Studies

The method of sampling for prey and predators developed during the study of the biological control of *A. piceae* has already been described (Clark and Brown, 1958). As part of this study, all stages of syrphids found on the sample areas have been recorded.

It has been very noticeable that the abundance of the various syrphid predators varies widely from year to year, and from place to place. From 1946

to 1959 larval populations of the three main species, *S. torvus*, *M. lapponicus*, and *N. coxalis*, ranged from very abundant to almost non-existent and a preliminary analysis of population data for the past 13 years from 111 sample trees in the Fredericton area indicates that there is no relationship between years, within years, or between trees for the two populations during that period. When host populations were high the syrphids were sometimes abundant, sometimes scarce, and when the host populations were low the same variations in syrphid populations occurred.

These variations in population occur in all three of the major species. *S. torvus* predominates in the early summer populations and *N. coxalis* late in the summer. *M. lapponicus* is generally much less numerous than *S. torvus* in early summer and occurs only in small numbers later in the season.

Control Value

In a previous paper (Clark and Brown, 1958) the control value of the introduced predator *Laricobius erichsonii* (Rosen.) (Coleoptera: Derodontidae) was discussed. In the work with *L. erichsonii*, check trees were those which had the complex of native predators (including the syrphids) feeding on *A. piceae*, as well as the chamaemyiid predator *Leucopis obscura* Hal. which had been introduced at an earlier date and was well established. It was shown that on the check trees an increase in *A. piceae* populations generally occurred during the season, and that the aestivosistens (summer) prey generation averaged 186 per cent of the hiemosistens (spring) generation. It was shown in another paper (Brown and Clark, 1957) that *L. obscura*, although sometimes very numerous on prey populations, was relatively ineffective largely because the larvae feed primarily on intermediate instars and adults, and only infrequently on eggs, and also because they feed too late in the developmental period of the prey to prevent a large amount of oviposition. Times of occurrence of syrphid larvae in the spring (mostly *S. torvus*), including the time of maximum abundance, almost coincide with those for *L. obscura* and, as stated above, prey eggs are not the preferred food of the later instars. Thus, *L. obscura* and the syrphids are very similar in their actions and the combined effect of their predation on the hiemosistens prey generation is not sufficient to prevent an increase in prey population in the aestivosistens generation.

In 1959 it was noted, from population sampling of host and predators, that on trees where both *L. erichsonii* larvae and syrphid larvae were present feeding on the hiemosistens generation, the aestivosistens generation was less numerous than on those trees on which only *L. erichsonii* larvae were present in the spring. *L. erichsonii* larvae feed later and reach peak numbers from two to three weeks later than the syrphid and *L. obscura* larvae. The combination of the early syrphid larval feeding, primarily on intermediate instars and adult prey, followed by *L. erichsonii* larvae which prefer prey eggs but also feed on the other stages, is apparently a very effective combination and, on the sample trees, results in an almost complete mortality of the hiemosistentes and the eggs laid by the adults of this generation. The following generation (aestivosistens) was thus either very small or non-existent on these trees.

Unfortunately, however, as noted previously, the population of *S. torvus* and *M. lapponicus* varies widely from year to year, being very abundant one year and practically absent in the following season. The effective combination of predators described above is at best very intermittent.

N. coxalis larvae, which occur more commonly in autumn, have much the same limitations. Their food preference is for intermediate instars and adults of

the prey, and the prey eggs are mostly left to hatch and produce the overwintering neosistens stage. Also, *N. coxalis* larvae are most numerous long after oviposition by the aestivosistens generation has begun.

Thus the general effect of syrphids is to reduce the rate of increase in the summer generation but the upward trend of the population is not reversed unless other factors, such as *L. erichsonii* or tree resistance, are present.

Other Syrphids on Infested Balsam Fir

Larvae

Several species of syrphid larvae, other than the three species considered above, have been found on balsam fir trunks infested by *A. piceae*. Most of these species are only encountered occasionally. Attempts to rear them to the adult stage have so far been unsuccessful.

1. (Fig. 13) A larva presenting a mottled appearance of a mixture of browns, whites, and yellows. The posterior respiratory processes are long, projecting posteriorly and about 45° dorsally, contiguous for their entire length, without a membranous cone-shaped base as in *N. coxalis* and with the apices enlarged to appear somewhat knob-like. This larva appears in June and continues to mid-July and is never as common as *S. torvus* or *M. lapponicus*. Larvae collected have probably been last instar and measured from ⅜ inch to ½ inch in length.

2. (Fig. 14) A dark yellowish-green larva, about ⅜ inch long. The dorsal blood vessel appears as a mid dorsal dark blue-black line with a narrow line of light blue-grey subdorsally. The posterior respiratory processes are prominent, completely visible from a dorsal view, with the basal portion contiguous, straw-coloured, darkening somewhat toward the apices which are broadly rounded. Only a few of these larvae have been found in mid-July and early October.

3. (Fig. 15) One unknown dark blue-black syrphid larva, about ½ inch long, was collected on June 24, 1958. This species has not been found again. The larva is covered with many large and small tubercles and presents a very rugose, spiny appearance. Two prominent long spine-like processes project postero-dorsally and slightly laterally from the posterior end. The posterior respiratory processes are small, black, hemispherical, contiguous at the base and visible from a dorsal view.

Adults

Metasyrphus wiedemanni (Johns.).—Atwood (1933) found larvae of this species in August as a predator on intermediate instars and adults of the aestivosistens prey generation. He noted that larvae were difficult to distinguish from *M. lapponicus* except by the time of feeding. Adults have been collected on infested balsam fir in May, June, and July.

The following species have been collected as adults on infested balsam fir but have not been reared from larvae collected on fir.

Syrphus ribesii L. — September
Syrphus ribesii vittafrons Shan. — August
Toxomerus geminatus (Say) — September
Neocnemodon sp. — June, August, September.

In 1954 a total of 703 adults of a mixture of the European species *Neocnemodon latitarsis* (Egg.) and *N. pubescens* D. & P.-W. were released at Fredericton. Neither species has been recovered and the introduction was apparently unsuccessful.

Summary

1. Three common native predators of *A. piceae* are described to permit field identification of all stages: *Syrphus torvus* O. S., *Metasyrphus lapponicus* (Zett.), and *Neocnemodon coxalis* (Curr.).
2. Their seasonal histories in relation to the prey are outlined. All are bivoltine but only one generation feeds extensively on *A. piceae*: *S. torvus* and *M. lapponicus* on the hiemosistens prey generation in early summer and *N. coxalis* on the aestivosistens generation in late summer and autumn.
3. Populations of the three syrphids have varied greatly from year to year and place to place with no clear relation to prey density.
4. Feeding habits limit their capacity to control *A. piceae*. They reduce the rate of increase but cannot reverse the upward trend of the adelgid population in the summer generation unless other factors are also present.
5. Eight species of parasites are recorded. Only one species parasitizes all three hosts.
6. Three species of syrphids which are occasional predators of *A. piceae* are briefly described and a number collected as adults on infested trees are listed.

Acknowledgments

We wish to express appreciation to the following officers of the Insect Systematics and Biological Control Unit, Entomology Research Institute, Ottawa, for identification of specimens of the predators and their parasites: J. R. Vockeroth (Syrphidae), G. S. Walley (Ichneumonidae), O. Peck (Pteromalidae), C. D. F. Miller (Encyrtidae and Pteromalidae). We also acknowledge the assistance of E. B. Bates of the Forest Biology Laboratory, Fredericton, who photographed the various stages of the predators. Thanks are also extended to R. E. Balch and R. F. Morris of the Forest Biology Laboratory, Fredericton, for critical review of the manuscript.

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The Olfactory Guidance of Flying Insects. II. Mosquito Repulsion

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A previous paper (*Canadian Entomologist* 40(2): 81-89, 1958) considered the general nature of an air-borne scent and suggested a mechanism by which a flying insect could be guided towards the source of an attractive odor. At first sight, it might seem that a repellent is merely an attractant with a minus sign, but this is an oversimplification, because an attractant may and often does bring the attracted insect in from a distance of a few miles, whereas the repellent has done its work if it removes the unwanted insect to a distance of no more than a few inches. The quantitative difference in the effect is so great as to imply a qualitative difference in the mechanism. On the naive view, the attractant draws the insect upwind and therefore the repellent should drive it downwind. A qualitative difference implies some third result, possibly a tendency to move the insect *across* the wind. This may, in fact, be the way repellents work in some circumstances, but it can scarcely be the whole story and is mentioned at this point merely to bring out the inherent difference between the attraction and repulsion of insects by odors.

A study has been begun of the behavior of mosquitoes (*Aedes aegypti*) in the presence and absence of various recognized mosquito repellents.

Preliminary experiments using a wind tunnel designed to produce a filamentous odor cloud of the repellent substance were unsatisfactory because of the infrequency with which any particular mosquito blundered into the affected zone and the quickness with which it then made its escape. The nature of the avoiding action was hard to discern.

A wind tunnel was therefore constructed in which the behavior of the mosquitoes could be observed and recorded by motion pictures. See Fig. 1. The observation chamber has a clear opening 20 by 24 inches and is nine inches from front to back. The back is translucent and can be lighted from behind so that the mosquitoes are photographed as silhouettes. This avoids any possible confusion between the insect and its shadow. A fan circulates air through the chamber and through a 1½-inch charcoal bed before returning it to the chamber. The temperature can be regulated by an electrical heating element, and the air can be given any desired humidity, or permeated with repellent or other vapors by passing it through a 1½-inch bed of porous material suitably impregnated with chemical. The porous material is contained in a sliding tray, visible near the bottom of Fig. 1, and arranged to slide in and out for quick changes in the atmosphere of the cage. The apparatus can be set in various positions so that the air stream moves horizontally or upwards or downwards through the chamber. Access to the interior is by way of openings in the side which can be closed by a plywood cover during the observations.

The camera is a Cine Kodak Special and is usually operated at 64 frames per second and at f 2.3 with an exposure of 1/130 second. Using Eastman Plus X Film, a moderate illumination of the background, with a Weston Meter reading of 13 to 25, is sufficient.

The advantage of using motion pictures to record the flight patterns is that the same flight can be observed over and over again, one insect can be followed regardless of the others, the movement can be slowed down, and the film can even be run backward. Thus the movements can be followed very well at least in two dimensions. Movement toward or away from the camera is harder to

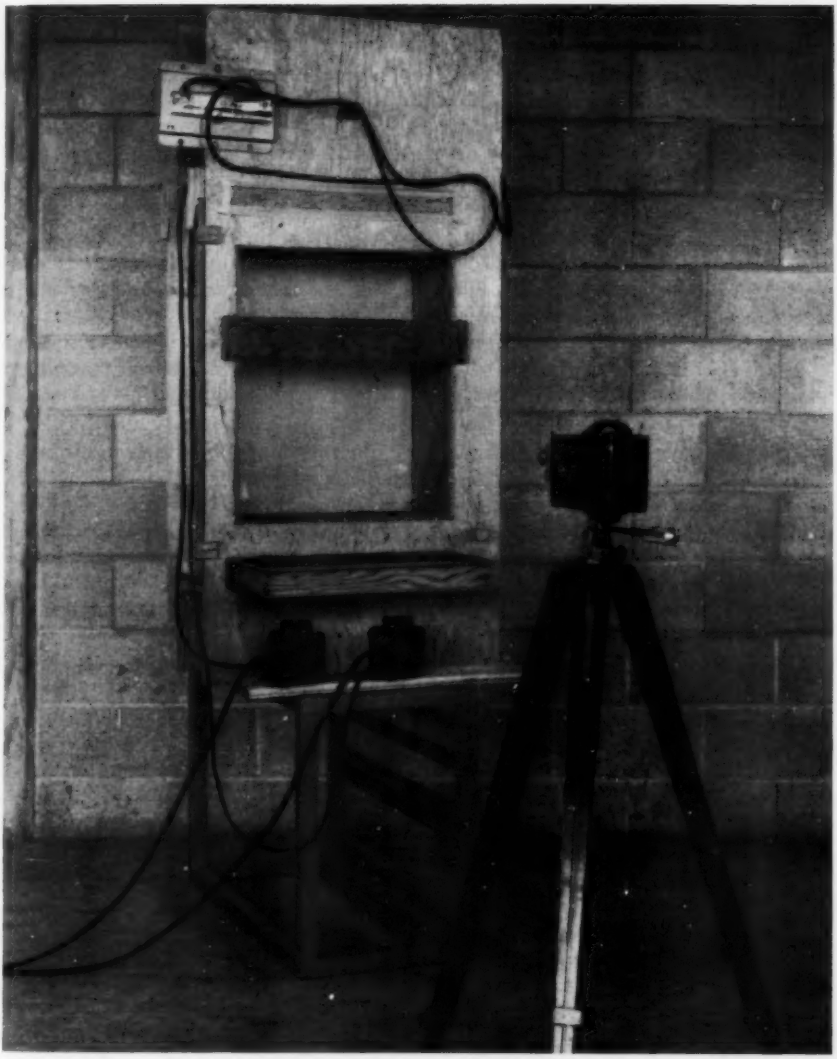


Fig. 1. Apparatus for studying reactions of mosquitoes to repellents. For description see text.

detect. Owing to the limited resolution of the film, the mosquitoes appear as rather fuzzy specks if the camera is set to photograph the whole of the 20 by 24 inch opening of the observation chamber. By moving the camera closer and using only part of the chamber, as shown in Fig. 1, the images are made larger and the outline of the insects is rendered quite distinct. However, it is desirable that the observation chamber should be as large as possible so that the flight may be free from wall effects.

The number of insects in the chamber was usually 100 to 200 and as a rule only about 25% were in flight when the pictures were being taken. Unless

otherwise stated, the temperature was about 27 to 28°C and the relative humidity 40 to 50%.

The mosquitoes used were *Aedes aegypti* and were reared from eggs kindly donated by Mr. L. Burgess of the Research Branch, Canada Department of Agriculture, Guelph, Ontario. Only females were used in the observation chamber and their ages varied from a few days to several weeks. They had not usually had a previous blood meal and had also been denied the usual sugar solution for at least a day prior to making the observations.

With visual observation of the film projected at 16 frames per second, the flight patterns remain bewilderingly complex and erratic, and, while it is plain that the repellent vapor alters the behavior, it is not easy to say precisely what the difference is. An old 16-mm. projector was therefore modified so as to project the film at one to two frames per second so that the paths of individual mosquitoes could be followed on the screen with a pencil. When necessary, an approximate indication of the speed could be registered by making a short transverse stroke across the track every ten frames.

Figs. 2, 4, and 6 show representative flight tracks of mosquitoes flying in air permeated with dimethyl phthalate and with the wind moving in various directions. Figs. 3, 5, and 7 show representative flight tracks with corresponding wind directions but with the insects in pure air. Fig. 8 shows some representative tracks modified by "612" (2-ethyl, hexanediol, 1,3), and Fig. 9 shows tracks modified by "Off" (a commercial preparation said to contain 40% of N,N-diethyl, m-toluamide). Fig. 10 shows tracks of mosquitoes flying in the presence of propylene glycol vapor, a non-repellent.

Inspection of these tracks shows that in the absence of the repellent vapor the number of turns made by the insect is large and the trace is tangled and complex. In the presence of the repellent the number of turns is much reduced and the insects fly a pattern of sweeping curves or almost straight runs. The flying speed is not markedly different, although when the films are viewed at 16 frames per second there is an impression of faster flight because with fewer turns the straight-line distance travelled is naturally greater. Fig. 11 shows a number of representative tracks with transverse lines marking equal time intervals.

The correlation of repellency with partial inhibition of turning appears to be quite clear. It may well prove to be a better criterion of inherent mosquito repellency than the usual one of "time to the first bite", which involves the various additional properties that make for persistency. The reported repellency ratings based on the duration of protection (W. V. King, "Chemicals Evaluated as Insecticides and Repellents at Orlando, Fla.", U.S.D.A., Agriculture Handbook No. 69, May, 1954) may, at times, be quite misleading. For example, ethyl acetoacetate is reported as non-repellent, but motion pictures of mosquitoes flying in air containing it showed a typical repellent response, and when applied to the skin the chemical gave complete protection during several minutes. Propylene glycol, on the other hand, gave almost no protection, and as can be seen from Fig. 10 it does not modify the normal flying pattern.

Watching the films[1] gives a distinct impression of an invisible barrier a few inches from the arm when lying horizontally, and there sometimes seems to be a tendency for the mosquitoes to linger in the region of the barrier. Sometimes, too, they make their escape by a pronounced upward zooming flight that is not seen in the absence of the repellent. When the arm is held vertically and protected by DMP the mosquitoes tend to approach more closely before taking the avoiding

1 Copies available on application to authors.

FIGURE 2

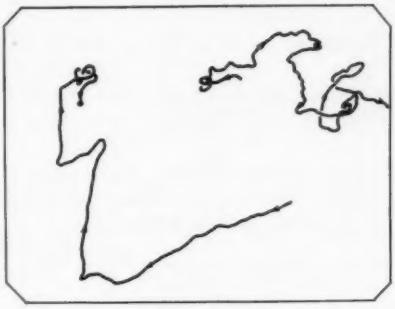


FIGURE 3

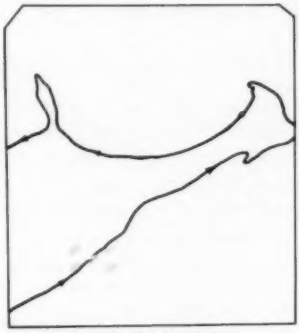


FIGURE 4

FIGURE 5

FIGURE 6

FIGURE 7

Figs. 2-7. Representative flight tracks of *Aedes aegypti* in air with (left) and without (right) dimethyl phthalate, and with different wind directions.

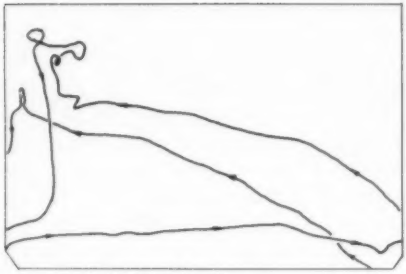
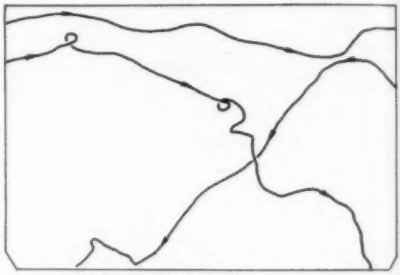


FIGURE 8



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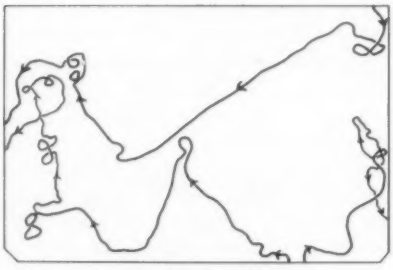

FIGURE 10

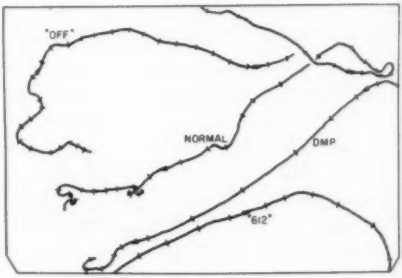

FIGURE 11

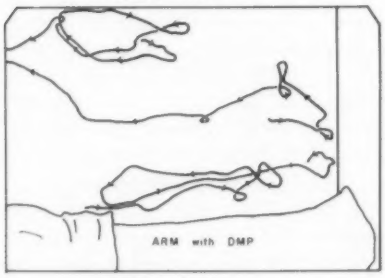

FIGURE 12

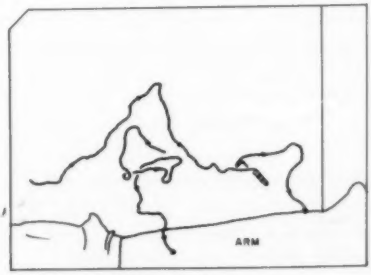

FIGURE 13

Figs. 8-13. Influence of various modifiers on flight tracks of *Aedes aegypti.*

action, which again is often a sudden zoom upwards, but sometimes a rather straight dash to the other side of the chamber.

Evidently the full mechanism of the avoiding action is still not clear, but inhibition of turning plays an important part in it. It will be recalled that in the earlier discussion of olfactory guidance it was postulated that inhibition of turning could result in attraction. Thus both attraction and repulsion may be effected by variations on the same theme. The difference in the effect may result from a difference in the duration of the inhibition. For attraction, the period of inhibition of turning should be of the same order of magnitude as the interval between the pulses of smell from different filaments of odorous material. For repulsion, the

period of inhibition should be much longer, so that the insect flies so far out of the odor cloud that it does not readily find its way back when the normal turning and search pattern is resumed. Such a mechanism would in some measure have an across-wind guiding action of the sort remarked on earlier.

It is clear that there are still many problems awaiting study, and it must be emphasized that this is a progress report on work which is under way but far from complete.

This work was made possible by an extra-mural grant from the Research Branch of the Canada Department of Agriculture and it is a pleasure to express our gratitude for this and for the continuing interest and encouragement we have received from Dr. B. N. Smallman and Dr. H. Hurtig.

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A New *Austromenopon* (Menoponidae-Mallophaga) Parasitizing Shearwaters (*Puffinus*-Procellariformes)

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A distinctive new species of *Austromenopon* from two species of shearwaters, *Puffinus kuhlii* (Scopoli) and *Puffinus leucomelas* (Temminick), is described herein. The new species is based on specimens collected from museum study skins and also from material lent to me by Dr. Theresa Clay, British Museum (Natural History) and the U.S. National Museum. I am indebted to Dr. Clay for the opportunity to examine material from the Meinertzhagen collection and to Dr. K. C. Emerson for reviewing this manuscript.

Austromenopon echinatum, new species

Male:—A large procellariform *Austromenopon*. Head as shown in Fig. 1, A. Outline relatively shallow and continuous, cephalic index 2 (head length measured at mid-line). Gular sclerite typical, lateral margins each with four (sometimes five) setae. Prothorax sharply angled at forward corner, lateral margin slightly incurved accentuating angular appearance. Posterior corner of metathorax with group of six to eight short stout setae. Metathoracic sternite roughly hexagonal, bearing two irregular rows of setae as well as being bordered with long setae. Third femora with typical loose setal brush (Fig. 1, B). Lateral tergal patches of stout pegs on apparent abdominal segments VI and VII, (Fig. 1, C). Pegs tending to curve anteriorly on segment VI and posteriorly on segment VII. Sternites IV-VI with loose setal brushes laterad. Genitalia centrally positioned, symmetrical, and very heavily sclerotized (Fig. 1, D).

Female:—About same size as male, not larger as is usually the case with genus. Chaetotaxy, except for terminal abdominal segments, similar to that of male, but without the abdominal pegs.

Measurements:— Averages and appropriate ranges in millimetres.

No. Specimens		Total Length	Head Length	Head Width	Paramere
ex *P. kuhlii*	3♂♂	2.1 (2.1-2.3)	0.70	0.30	0.25
	13♀♀	2.2 (1.9-2.5)	0.67	0.35	
ex *P. leucomelas*	3♂♂	2.2 (2.1-2.3)	0.70	0.35	0.27
	8♀♀	2.2 (2.0-2.5)	0.70	0.33	

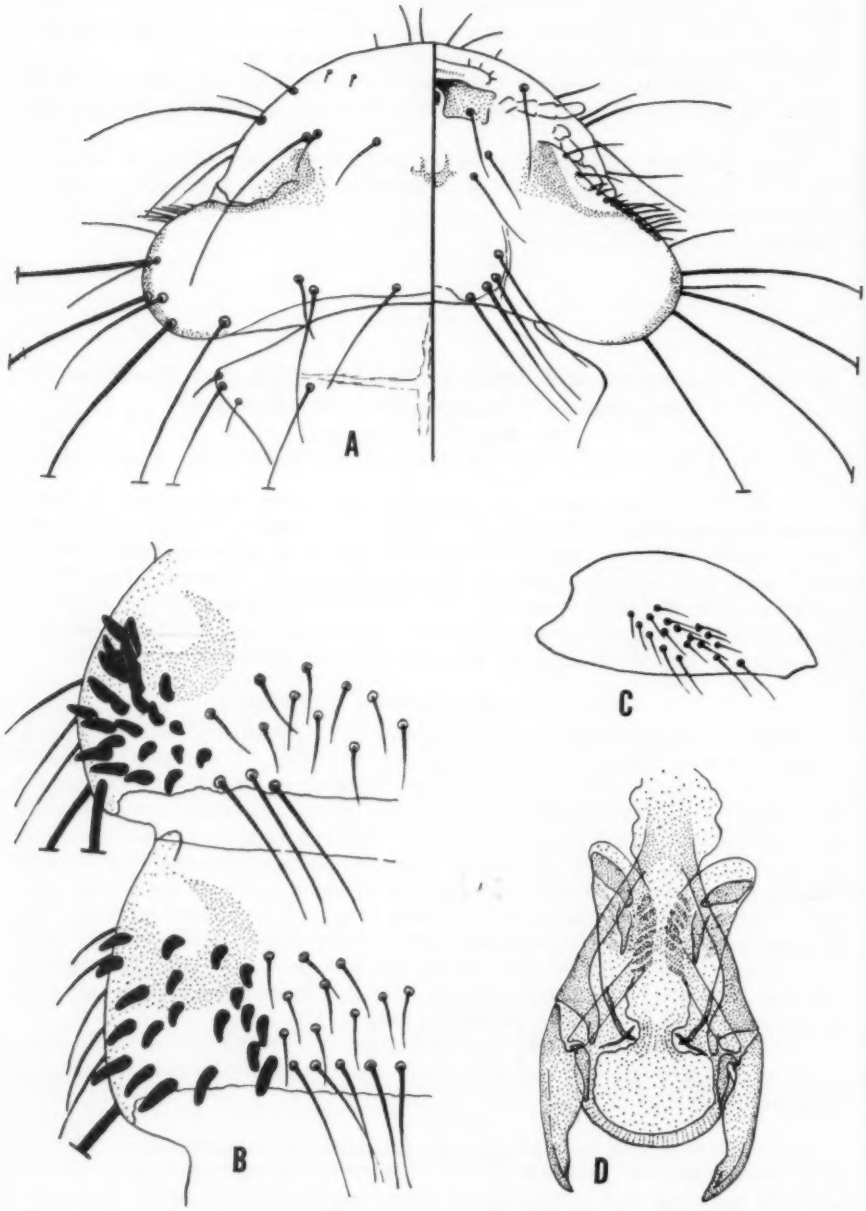

Fig. 1. *Austromenopon echinatum*, n. sp., holotype, male. A, Dorsal-ventral view of head; B, Pegs on tergites of abdominal segments VI and VII; C, Setal brush on ventor of third femora; D, Genitalia.

The differences in measurements between sexes and hosts are not significant. The samples are small statistically and these differences are well within the range of normal variation.

Type Host:—*Puffinus kuhlii* (Scopoli), Cory's shearwater.

Type material:—Holotype, male, allotype, female, five paratype males and 14 paratype females from *Puffinus k. edwardsi*, M.C.Z. skin #94293; one paratype male, three paratype females from *Puffinus k. borealis*, Canary Islands, Meinertzhagen slide #8200; seven paratype females from *Puffinus d. diomedeae* (= *Puffinus k. kuhlii*), Constantinople, Meinertzhagen slide #8199; and 20 paratype males and 20 paratype females from *Puffinus k. kuhlii*, Trinidad, B.W.I., U.S.N.M. material.

Other material examined included 12 mounted and 24 preserved specimens from *Puffinus leucomelas*, China Sea, taken off M.C.Z. skin #131515, and one female from *Puffinus leucomelas*, Japan, Meinertzhagen slide # 8201.

Holotype and allotype deposited in the Museum of Comparative Zoology. Paratypes will be deposited in the British Museum (Natural History), the U.S. National Museum and the American Museum of Natural History.

Discussion:—This large member of the genus *Austromenopon* is readily distinguished from all other described species by the presence of the patches of prominent pegs on the male abdomen.

Puffinus kuhlii and *Puffinus leucomelas* are considered to be closely related. Their ranges overlap in the Indian Ocean. Specimens of *A. echinatum* from the two host species are so similar that they cannot be separated into subspecies, arguing a very close relationship for their hosts. These two hosts also share similar and possibly conspecific populations of lice of the genus *Saemundssonia*. However, lice of the genus *Halipeurus* on these birds are distinctly different species, although more closely related to each other than to any of the other species of the genus. On the basis of their parasites then it may be suggested that the populations of *P. kuhlii* and *P. leucomelas* do not come into contact with one another but that they are very closely related.

(Received April 13, 1960)

Descriptions of Immature Forms and Biology of *Xylotrechus colonus* (Fab.) (Coleoptera: Cerambycidae)[1]

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During current studies of Cerambycidae at Laniel, Quebec, new information on the immature forms and biology of the common woodborer, *Xylotrechus colonus* (Fab.) was obtained. This species belongs to the tribe Clytini of the subfamily Cerambycinae, and was first described by Fabricius in 1775 as *Callidium colonus*. Packard (1890) described and figured the larva, pupa, and adult in a general way; the mature larva was described in detail by Craighead (1923). Synonomy and adult description were given by Hopping (1932).

Study Material

On July 6, 1955, a five-inch red oak was felled, cut up, and left for possible infestation near Laniel. The pieces were examined in late September, 1955, when three cerambycine larvae ranging from 7.0 to 10.6 mm. in length were found in the bark, and again on June 7, 1956, when seven more larvae ranging from 4.3 to 13.0 mm. in length were preserved. On the latter occasion, four of the sticks were brought in and caged at Laniel Field Station. On June 10, 1957, these yielded two full-grown larvae and a pupa, which gave rise to a *X. colonus* adult 16 days later.

In late August, 1957, piles of yellow and white birch bolts along a road clearing near Mattawa, Ontario, were examined and yielded larvae that were tentatively identified as *X. colonus*. Four pieces of yellow birch and two of white birch were caged at Laniel. Emergence of *X. colonus* began on August 6, 1958, and on the following day the bark was removed from the sticks. Larvae, pupae, and adults were obtained in this way, as well as parasite cocoons, and diseased larvae and pupae. The adults were caged with a piece of yellow birch cut in the spring of 1958. Mating and oviposition occurred readily in the cage, and eggs and first-instar larvae were obtained.

All insect material described in this paper is in the Cerambycidae Collection at Sault Ste. Marie, under the collection numbers C32.4.1, C32.4.2, and C32.4.3.

Descriptions of Immature Stages

Mature Larva (Fig. 12)

The following description, which appears adequate in most respects, was given by Craighead (1923). Additions based on examination of material during the present study are given in parentheses.

"*Form* semirobust, contracted, subcylindric, tapering to last few abdominal segments; integument firm, rather dull, densely covered with fine, soft, lemon-coloured hairs.

"*Head* trapezoidal, gradually tapering anteriorly; mouth-frame corneous, very finely wrinkled, reddish-brown; labrum rather thick, soft, suborbicular, widest behind middle, with very short hairs; mandibles dull black, short, tapering rapidly to apex, basal piece about one-third length of apical, no fovea on outer face; first antennal joint about equal to last, much shorter than second, supplementary distinct; one distinct ocellus contiguous with base of antenna (usually separate from base of antenna in present material, Fig. 7); gena tapering, not shouldered, bearing several very fine hairs. Ventral mouthparts rather fleshy; all joints of

[1] Contribution No. 588, Forest Biology Division, Research Branch, Department of Agriculture, Ottawa, Canada.

labial and maxillary palpi subequal, basal joints of latter transverse; process of palpifer short, distinct, subfossal spine small.

"*Prothorax* rectangular, about twice as wide as long, thick; four distinct ochraceous tergal plates; lateral regions thickly beset with short orange hairs, those on the sternum longer except for the large, suborbicular, glabrous eusternal spots; pronotum wider than long; median suture slightly impressed, punctured and sparsely hairy anteriorly, posteriorly covered with dark-ochraceous, velvety pubescence and a posterior band on pro-eusternum; mesonotum, metanotum, and anterior half of sterna also covered with velvety pubescence; ventral-latero sutures a mere notch. Legless (all mature larvae examined in this study possessed rudimentary legs consisting of a minute tubercle with a sclerotized tip. Two sclerites occur at the base of the tubercle, and the tubercle shows evidence of rudimentary segmentation, Fig. 10).

"*Abdomen*: ampullae large, transverse, flat, dull, very finely granulate, surrounded by velvety pubescence; ventral bearing a longitudinal median stripe of velvety pubescence, no distinct impressions (ampullae marked by a transverse and two lateral furrows, two glabrous spots near middle, and four glabrous streaks or folds on posterior half, Fig. 8; ventral granulate except for median stripe, marked with a pair of deep lateral folds, Fig. 9). Pleural disc indistinct. Spiracles narrowly oval to broadly oval, peritreme thin."

First Instar

Form as in mature larva, except that prothorax is not so thick, and head is more salient. Mouthframe heavily sclerotized except in gular region, which is unconsolidated. Antennae well developed, salient, supplementary process subcylindrical (Fig. 1). One ocellus behind each antennal socket. Mouthparts as in mature larva except for lack of sclerotization on labium and maxillae.

Pronotum asperate on posterior half, with sparse, long setae on the anterior margin and lateral areas, midline lightly impressed, granulate. Mesonotum and metanotum lightly asperate posteriorly. Legless, but with a small, close group of four short, stout setae where legs would be. Mesothoracic spiracles biforous.

Abdominal ampullae undefined. Hatching spines (egg-bursters of authors) present on abdominal segments IV to VIII inclusive, largest on VII (Figs. 2 and 3). Abdominal spiracles normal (Fig. 4), except those on segment VIII and sometimes those on segment VII, which are biforous (Figs. 5 and 6). This is different from at least two other *Xylotrechus* species, *sagittatus* (Germ.) and *undulatus* (Say), in which all first-instar spiracles are biforous.

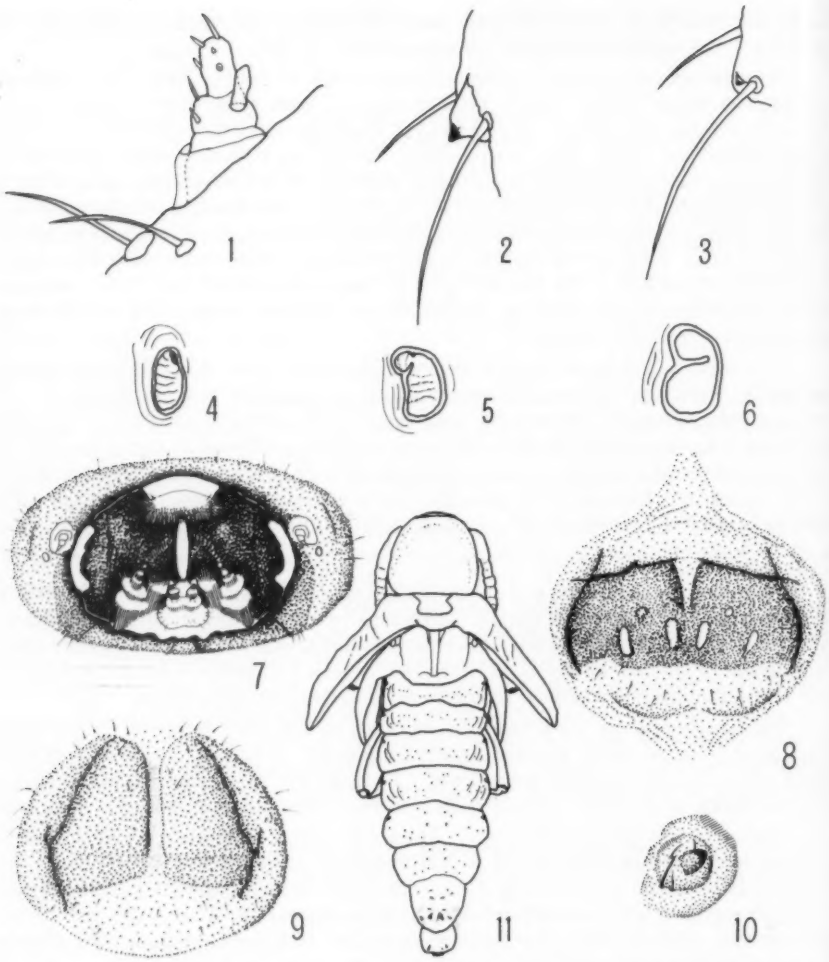
Pupa (Fig. 11)

Length up to 15 mm.

Head: vertex barely visible from above; frons glabrous, transversely furrowed; clypeo-labrum triangular.

Thorax: pronotum beset with numerous small spines each bearing a subapical seta, otherwise glabrous, not rugose as stated by Duffy (1953) although it may appear so when rugosities of the imago show through the pupal integument. Mesonotum and metanotum nearly glabrous, shining, scutellar groove prominent. Elytra divergent, hind wings curved under body, enclosing bases of hind legs. Hind femora slightly divergent, extending to fourth abdominal segment.

Abdomen: inflated, widest at segment IV. Terga armed with spines which, in general, become progressively larger posteriorly, and some of which bear apical or subapical setae. Seventh tergum tapering posteriorly, hind margin rounded, marked with a transverse row of four spines directed forward. Eighth tergum



Figs. 1-11. 1, *X. colonus*, first instar—ventral view of right antenna and ocellus. 2 and 3, First instar—dorsal views of left hatching spines on abdominal segments VII and VIII, respectively. 4, 5, and 6, First instar—ventral views of right spiracles on abdominal segments VI, VII, and VIII, respectively. 7, Mature larva—front of head. 8, Mature larva—dorsal ampulla of VIth segment. 9, Mature larva—ventral ampulla of VIth segment. 10, Mature larva—rudimentary limb. 11, Pupa.

slightly inflated at tip, bearing two to four smaller spines near the hind margin. Segment IX retracted, barely visible from above. Sternites glabrous but for a few very minute setae. Functional spiracles present on first five segments, vestigial on segments VI and VII.

Distribution

Aside from Ontario and Quebec, this species has been recorded from Massachusetts, New York, New Jersey, Pennsylvania, District of Columbia, West Virginia, Virginia, Florida, Indiana, Ohio, Illinois, and Mississippi (Blackman and

Stage, 1924). Hopping (1932) examined specimens also from Kansas, Michigan, and Iowa. It is probably common throughout the hardwood forests of Eastern Canada and eastern United States.

Habits

Emergence of adults at Laniel occurred in late June and August; therefore, the beetles are probably active throughout most of the summer in Eastern Canada. The adults are fairly strong, fast fliers. They were not observed to feed, although sugar and water and birch foliage were provided for them in the cages.

Mating and oviposition took place during the afternoon and on warm evenings. The eggs, which are short, stout, and opaquely white, were laid singly or in groups of up to six, lightly glued to the substrate. No preparation of the bark, such as chewing or drilling, was observed. In red oak, and sometimes in yellow birch, the eggs were often placed in the inner bark at the cut ends of the sticks, but more frequently were laid under the rough bark scales around old branch scars or simply on the underside of shreds of outer bark. The egg stage occupied roughly three weeks. Blackman and Stage (1924) reported at least 19 eggs laid in a single crack in the bark of a hickory tree.

Unless oviposition occurs in the end of the log, the first-instar larvae must bore through the outer bark into the inner bark which is their food. Gallery type appears to vary with the species of tree infested. In red oak, the galleries are elongate and fairly straight, and the surface of the wood is deeply scored (Fig. 13). This may result from the relative thinness of the inner bark, and the coarse bast fibres. In yellow birch, whose inner bark is thick and fairly homogeneous, the wood is scored only lightly, if at all. The galleries are tightly packed with granular frass.

Pupal chamber construction also appears to depend on bark thickness. In red oak, and to some extent in white birch, pupation took place in shallow cells excavated in the sapwood (Fig. 13), whereas in yellow birch it occurred mainly in the inner bark at the end of the gallery (Fig. 15). In one instance, the pupal stage lasted for 20 days. The adult emerges by chewing an oval hole through the bark.

The life history of this species was completed in roughly 23 months at Laniel, in the northern part of its range. Development time in the eastern United States has been recorded as one year (Craighead, 1923), but also as long as three years, depending on temperature and the condition of the wood (Blackman and Stage, 1924).

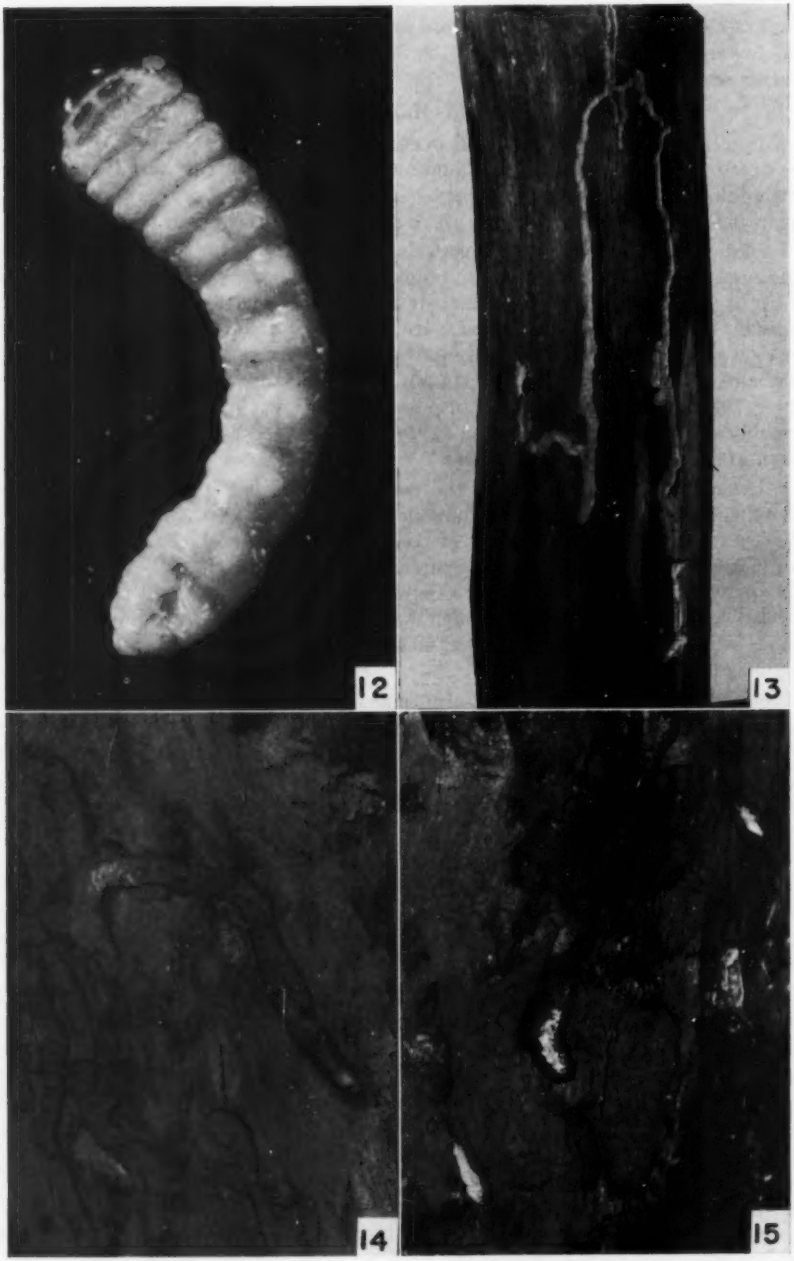
The range of length (6.1 to 22.6 mm.) of larvae found in yellow birch logs indicates that the same material had been infested in at least two different seasons, possibly three.

Host Trees

X. colonus has been recorded as breeding in black oak, white oak, hickory, chestnut, ash, elm, sugar maple, and hemlock. Chagnon (1940) gives beech as a host in Quebec. In the present study, red oak, yellow birch, and white birch were infested under natural conditions. It was observed that where both white and yellow birch were available to the insect in the same pile, only the yellow birch was infested. Infestation in white birch only occurred in pure piles of that species, and even then it was light.

Damage

The presence of these insects in valuable hardwood logs need be no cause for apprehension, since their feeding is largely restricted to the inner bark, with



Figs. 12-15. 12, *X. colonus*, mature larva. 13, Galleries in red oak, showing pupal chambers in wood, as well as scoring of the wood-surface. 14, Galleries in inner bark of yellow birch; pupal cell at the end of gallery occupied by cocoon of parasite, *Helconidia ligator*. 15, Galleries and pupal cells in inner bark of yellow birch; pupa in centre infected by *Isaria farinosa*, healthy pupa at upper right.

only negligible penetration of the wood in some cases. However, they may do indirect damage by facilitating the entry of wood-staining and wood-rotting fungi into the logs.

Felt (1905) and Blackman and Stage (1924) record infestations of *X. colonus* in living hickory trees. Felt believed that a large hickory had been killed by a heavy invasion by this species. It is always possible that living trees may be killed by massive, often repeated, attacks by a borer that is considered to be a usually secondary insect. Very often, however, such trees are in a sickly condition, as in the case reported by Blackman and Stage.

Parasites

Chittenden (1894) found *X. colonus* parasitized by the ichneumonid *Xylonomus rileyi* Ashm. and Felt (1905) reported parasitism by *Melanobracon simplex* Cress., and the ichneumonid *Arotes decorus* Say. In the present study, the braconid *Helconidia ligator* (Say) was found as pupae in the pupal chambers of *X. colonus* (Fig. 14). The parasites emerged at about the same time as the beetle adults.

In addition, a small number of larvae and pupae were found to be infected by an entomogenous fungus, *Isaria farinosa* (Dicks.) Fr. (Fungi Imperfecti). Infected specimens exhibited the typical mummified appearance, and were covered by a white mycelium (Fig. 15). An as yet unidentified fungus which gave rise to a green mycelium when cultured and which may be entomogenous, was also found infecting a small number of specimens.

Acknowledgments

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(Received October 2, 1959)

On the Life History of the Douglas-fir Cone Moth, *Barbara colfaxiana* (Kft.) (Lepidoptera: Olethreutidae), and one of its Parasites, *Glypta evetriae* Cush. (Hymenoptera: Ichneumonidae)[1]

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Introduction

The Douglas-fir cone moth has been reported causing damage to cones and seeds of Douglas fir for a number of years; reports of seed loss range from light to almost 100 per cent. The insect occurs throughout the range of the host in British Columbia, the Pacific Coast States, and the Rocky Mountains.

Observations recorded here were made during 1957 and 1958 in the Cowichan Lake area of Vancouver Island, and 1959 in the interior of British Columbia.

Barbara colfaxiana was described by Kearfott (1907) as *Evetria colfaxiana*. Heinrich (1923) revised the family Olethreutidae and created a new genus *Barbara* of which *E. colfaxiana* was the type species. He divided the genus into three varieties of the type and a species considered to be an aberrant form of *colfaxiana*. All of these feed in cones of Douglas fir except one of the varieties, *B. colfaxiana siskiyouana* (Kft.), which attacks cones of several species of *Abies*. Another species, *B. mappana* Freeman, feeds in cones of Engelmann spruce.

The larvae of *B. colfaxiana siskiyouana* and *taxifoliella* were described by Margaret MacKay (1959).

In 1900, Cooley observed the actions of a lepidopterous cone-borer in cones of Douglas fir. He published a bulletin (Cooley, 1908) on the Douglas spruce cone moth which he called *Cydia pseudotsugana* Kft. Keen (1953) was sure that the insect was misidentified and that Cooley's report was the first to be made on *B. colfaxiana*. The habits of the insect described by Cooley agree very closely with those of *B. colfaxiana* as observed by the writer.

More recently, Radcliffe (1952) and Keen (1958) have published accounts on the insect.

Life History and Habits

The adult (Fig. 1) emerges from its pupal case in the cone early in the spring. The time varies with location and elevation, but emergence commences shortly after the Douglas-fir flowers burst their buds, when pollen is being shed. At Cowichan Lake, B.C., this is about the middle of April. In 1958, adults were active from April 20 to May 18. Insects reared in the laboratory lived from three to 16 days.

The moth flies and oviposits only in the evening. Females were observed ovipositing from 6:00 p.m. to 8:15 p.m., P.S.T. The insect hovers around the extremities of the branches and settles on the foliage — none was observed to alight directly on a cone. After settling, the insect walks over the foliage, feeling continually with the ovipositor. When a cone is located oviposition commences. The insect stands on the bract, usually facing along the cone; from this position eggs are deposited on the outer surface of the bract. Occasionally eggs are found on the inner surface of the bract; this occurs when the female, instead of standing along the length of the cone, stands perpendicular to the length and curves the abdomen around the edge of the bract to the inner side, where an egg is deposited.

[1]Contribution No. 626, Forest Biology Division, Research Branch, Department of Agriculture, Ottawa, Canada.

In areas of high infestation a number of eggs may be deposited on a single bract (Fig. 2). A total of 387 eggs were counted on 22 cones on one tree, averaging 17.6 eggs per cone; the greatest number on a single cone was 44.

The insect oviposits on cones throughout the height of the tree. Four trees about 35 feet in height, at Oyama, B.C., were sampled from top to bottom to compare infestations at different heights. Cones were taken from two branches on opposite sides of the tree in each of five whorls. There was little difference between the percentage of cones infested at each level. Mean differences for the five levels on all trees ranged from 21 to 36 per cent. Differences between trees ranged from 19 to 57 per cent.

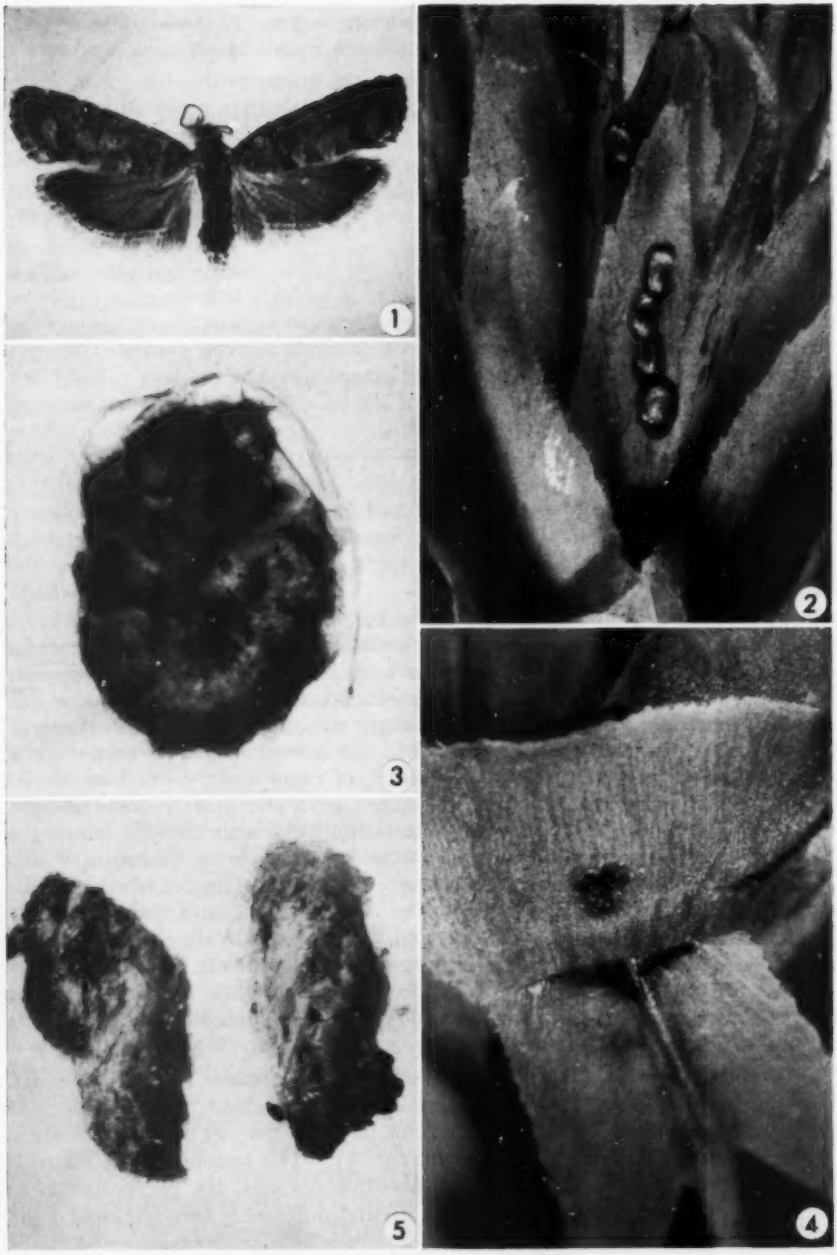
The egg is pearl colour when first laid. It has an uneven reticulate surface and averages 0.85 mm. in length and 0.71 mm. in width. It is attached firmly to the surface of the bract by an area of glue which can be seen clearly around the margin of the egg (Fig. 2). As the embryo develops, the egg gradually changes in colour from the original pearl colour to orange and then to black. The black is due to the colour of the head capsule of the fully developed embryo showing through the almost transparent egg shell (Fig. 3). The incubation period is from two to three weeks. Hatching commences about May 15 in the Cowichan Lake area.

As shown in Fig. 3 the fully developed embryo lies in a curled position. When development is complete the larva bursts the extremely delicate egg shell and proceeds to locate a feeding site; the egg shell remains for some time on the bract.

The young larva, which is only about 2 mm. in length, crawls up the bract until it reaches the angle between a bract and scale; if unable to locate this site it soon perishes. The cone scale is very pubescent during this stage of development and unless the larva can wedge itself between a bract and scale and thus penetrate the pubescent layer it is unable to start feeding on scale tissue. All larval entries observed on Vancouver Island were made in this manner (Fig. 4). Observations made by Radcliffe (1951) as to larval point of entry agree with those above. Keen (1958) reports that "The newly hatched larva immediately bores through the supporting bract and enters the cone through the scale directly below the bract . . . ". Examination of 100 larval entries into cones in the Okanagan Valley of British Columbia in 1959 by the writer showed the situation described by Keen to occur frequently. Fig. 6 illustrates the relative positions of different points of entry into bract or scale of cones from the Okanagan Valley. No. 1 shows an entry made into the scale after feeding on the edge of the bract. Nos. 2, 3, and 4 are entry holes made from different positions below the bract. No. 5 which is not illustrated is an entrance made in No. 4 position but the hole is made through the bract and then into the scale.

As shown in Table I, 45 per cent of all entries were made through the bract, or a portion of it (nos. 1 and 5) before entering the scale. The remaining 55 per cent were made directly into scale tissue but only five per cent were made in the position described for coastal entries (no. 4). The reason for this variation in point of entry is not known. Further investigations will be conducted to determine, if possible, whether there are varietal differences between coastal and interior cone moths, and also whether differences in cone development between Coast and Interior influence the young larvae.

Mortality at this stage of development is high. Many larvae are unable to locate the point of entry and thus starve. Of 313 eggs which hatched, only 172,



Figs. 1-5. *Barbara colfaxiana* (Kft.) 1. Adult; 2. Eggs; 3. Fully developed embryo; 4. Larval entrance hole (Coastal); 5. Cocoons.

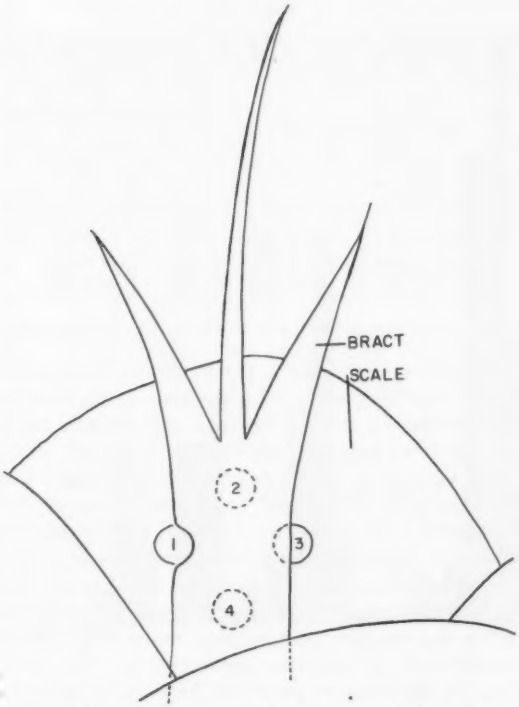


Fig. 6. Points at which larval entry holes were made into cones in Interior B.C. 1. Through portion of bract into scale; 2. Into scale from below bract; 3. Into scale from below edge of bract; 4. Same as 2 but lower on scale.

or 55 per cent, managed to establish in cone scales. Many larvae perish in the first instar shortly after entering the cone scale due to excessive flow of pitch in the feeding tunnel.

Once established, the larva feeds on the surface of the scale for several days, gradually tunnelling into the tissue and leaving a small amount of frass at the point of entry. Growth is rapid and the body increases greatly in size before the first moult. Prior to each moult the larva spins a delicate protective screen within the feeding chamber behind which moulting takes place.

TABLE I

Position of *B. colfaxiana* larval entries into cones collected in Okanagan Valley, B. C., July, 1959

Point of entry (see Fig. 6)	No. of entries
1	43
2	27
3	23
4	5
5*	2

*Same position as No. 4 but entry is through bract.

TABLE II

Periods during which different instars of *B. colfaxiana* were present in cones, and head-capsule widths of 375 larvae, Cowichan Lake, B. C. 1958

Instar	Period	Head-capsule width (mm.)		
		Range	Mean	Standard deviation
1	May 20 – 29	0.209 – 0.313	0.279	0.024
2	May 23 – June 11	0.381 – 0.503	0.440	0.023
3	May 27 – June 12	0.531 – 0.783	0.689	0.049
4	June 3 – July 15	0.822 – 1.310	1.119	0.080

During the first and second instars, food consists of scale tissue. The larva continues to burrow into the cone and by the time it has developed to the third instar feeding is concentrated around the cone axis. Seeds are now included in the menu. When the larva first encounters seeds it is small enough to enter and feed within the seed, devouring the entire endosperm. Later, seeds are excavated from an opening in the end of the seed, or devoured entirely. Feeding tunnels wander at random around the cone axis. Several late-instar larvae may feed in the same tunnel without showing cannibalistic tendencies.

Head-capsule measurements were taken on a number of living larvae. This was accomplished by removing them from cones, anaesthetizing them with carbon dioxide while taking the measurement, and re-establishing them in cones in the insectary for measurements after further development. The larva passes through four instars during the approximate period of May 20 to July 15. Periods when larvae from each of the instars were present in cones at Cowichan Lake, 1958, are shown in Table II along with head-capsule widths of 375 larvae. A histogram of the frequency distribution of the head-capsule widths is presented in Fig. 7.

At the completion of feeding, about the middle of July, the mature larva constructs a tough cocoon adjacent to the cone axis in the feeding tunnel, and pupates. The cocoon (Fig. 5) becomes heavily coated with pitch.

The insect remains dormant in the cone until April or May of the following year when the adult moths emerge to oviposit in the new cones. In the Cowichan Lake area the majority of the cones remain on the tree for at least one winter following maturity, which means that the insect usually overwinters on the tree rather than on the ground. The moths do not all emerge in the spring following the year of pupation. In 1958 seven per cent (14 of 197) of the pupae in rearing remained in diapause until 1959. Keen (1958) reports dormancy extending for three winters.

Cones collected at a number of points in the interior of British Columbia at completion of larval feeding were examined for information on seed loss. The data in Table III show that seed losses where there was one larva per cone, ranged from 60 to 100 per cent and averaged 65 per cent; when there were two larvae per cone losses ranged from 85 to 90 and averaged 86 per cent. The only cone infested with three larvae suffered 100 per cent loss.

Parasites

Numerous parasites have been reared from infested Douglas-fir cones and reported as parasites of *B. colfaxiana*. These require verification as the cones contain several other species of phytophagous insects which may be parasitized.

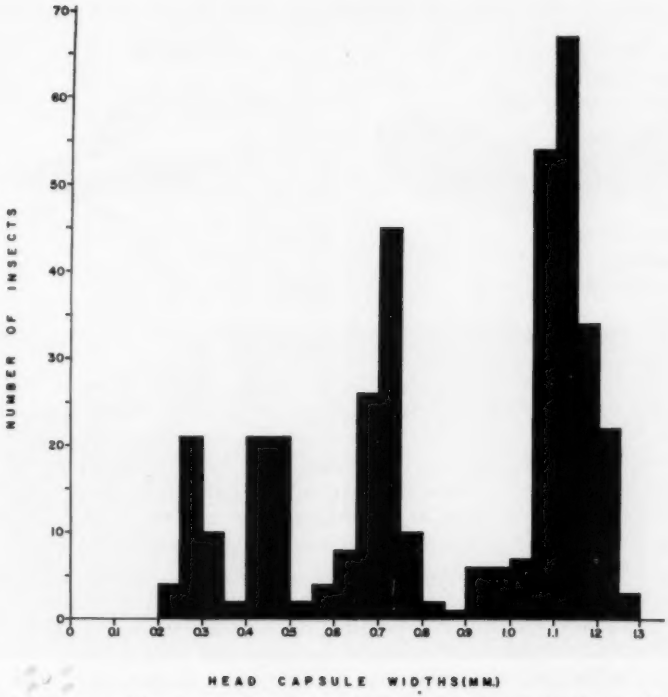


Fig. 7. Histogram of frequency distribution of *Barbara colfaxiana* head capsule widths.

TABLE III

Seed loss caused by one, two or three *B. colfaxiana* larvae per Douglas-fir cone in the Interior of British Columbia, 1959

Locality	No. cones examined	No. cones infested with			Seed from infested cones		
					Total	Destroyed	
		1 larva	2 larvae	3 larvae		No.	%
Boston Bar	19	1			20	20	100.0
Kamloops	40	10			396	256	64.6
"			2		136	116	85.3
Monte Lake	40	8			356	216	60.7
"			5		292	248	84.9
"				1	56	56	100.0
Vernon	38	7			248	176	71.0
"			2		84	76	90.5
Penticton	30	12			280	212	75.7
Keremeos	30	8			344	248	72.1
Damage by 1 larva/cone		46			1020	668	65.5
" " 2 larvae/cone			9		512	440	85.9
" " 3 larvae/cone				1	56	56	100.0

In this study the following parasites have been reared from *B. colfaxiana*:

Parasite	*Occurrence*
Ichneumonidae	
Glypta evetriae Cush.	Very common
Eulophidae	
Elachertus sp.	Fairly common
Tetrastichus strobilus Burks	Fairly common
Braconidae	
Apanteles sp.	Rare
Pteromalidae	
Platymesopus sp.	Rare
Tachinidae	
Pseudoeribia sp. nr. *tothilli* Curr.	Rare

G. evetriae (Fig. 8) was observed to be an effective parasite. It has previously been reported as a parasite of *B. colfaxiana* in Oregon and Montana (Townes, 1951) and also California, Colorado, and Washington (Keen, 1958). Johnson and Winjum (1960) observed it in their studies in Washington.

Adult emergence commences about 10 days after that of the host. Adults are present for a period of about one month from the first week in May. They were observed to be active in the field from 7:30 a.m. until late evening.

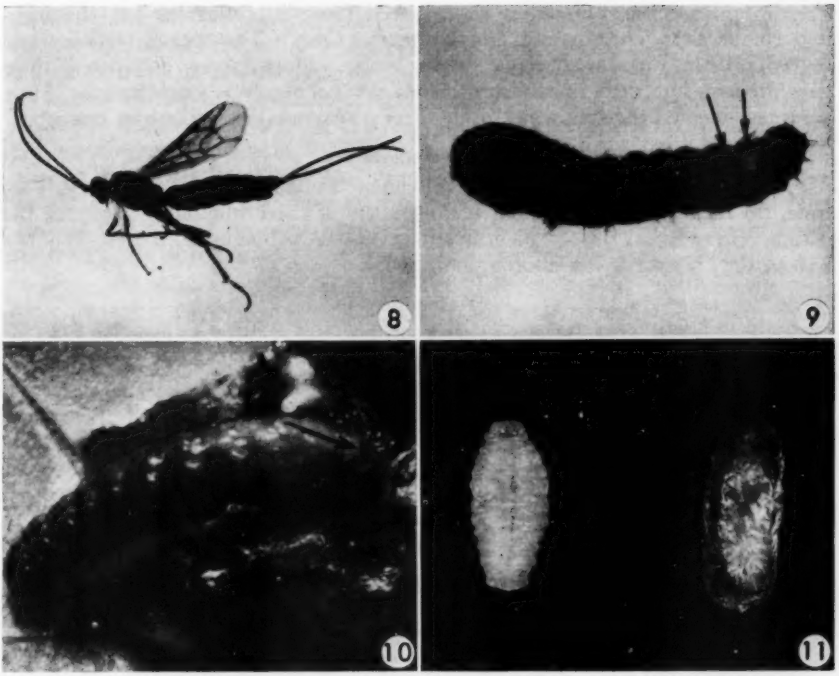
The female walks quickly over cones moving her antennae rapidly up and down. As soon as she detects the presence of a host larva, she draws her ovipositor underneath her so it is pointing forward between the fore legs. She then pushes the ovipositor underneath the bract and after making several short sharp jabs, withdraws the ovipositor allowing it to assume its normal position. During the operation, which requires less than one minute, an egg is deposited within the abdomen of the host larva. A wound which is readily visible is inflicted on the young larva (Fig. 9); apparently no selection is made on the basis of whether the host is previously parasitized or not because as many as eight parasite wounds were observed on a single larva. Eggs are laid only in early-instar larvae before they become entrenched in the cone.

The egg hatches and the larva develops within the body of the host. Only a single parasite develops in a host regardless of the number of eggs deposited; the others are killed in some way and their remains are readily visible in the host body throughout the remainder of larval development (Fig. 10).

The parasitized host feeds and develops in the normal way until the cocoon is constructed. When the larva is ready to pupate it is killed by the parasite. The parasite larva constructs a delicate semitransparent case (Fig. 11) within the cocoon constructed by the host larva and remains in this as a larva until spring of the following year. A few were observed to emerge in the fall shortly after killing the host.

In the Robertson River Valley near Cowichan Lake parasitism was high in 1958. Fifty-six per cent (96 of 172) of the larvae which established successfully were killed in the first instar as a result of wounds from oviposition by *G. evetriae*.

Examination of cone moth cocoons in 1958 and 1959 yielded the following information on parasitism by *G. evetriae;* in 1958, 197 cocoons were examined and 74 (38 per cent) were parasitized; in 1959, 41 of 48 cocoons (85 per cent) in the Robertson River Valley and 12 of 22 cocoons (55 per cent) at Colwood contained parasites.



Figs. 8-11. *Glypta evetriae* Cush. 8. Adult; 9. Ovipositor wounds to first-instar *B. colfaxiana* larva; 10. Remains of dead parasites in body of fully developed host larva; 11. Larva; in semitransparent cocoon (right), naked (left).

Of the 313 cone moth eggs mentioned previously which hatched on a tree in the Robertson River Valley in 1958, only two per cent lived to pupate. The mortality was not due entirely to parasitism by *G. evetriae;* 172 established successfully in the cone, 76 lived beyond the first instar, and six, or two per cent of the original hatch pupated. Ninety-two per cent of the larvae from this tree, which lived to spin cocoons, were parasitized by *G. evetriae.*

Summary

The first report on what was almost certainly the Douglas-fir cone moth, *Barbara colfaxiana* (Kft.) was made in 1900 by Cooley.

The adult moth lays its eggs on the bracts of Douglas-fir cones during April and May. Oviposition occurs on cones throughout the height of the tree. The eggs hatch in two to three weeks and the young larvae tunnel into the cone feeding on scale tissue and seeds. Differences in points of entry into the cone by larvae from the interior and the coast were noticed. The larvae feed from early May until about the middle of July, during which period they pass through four instars.

Sixty-five per cent of the seeds in infested cones were destroyed when a single larva was present; multiple infestations caused heavier losses.

Pupation takes place in a tough cocoon in the feeding tunnel within the cone, in July. The insect overwinters in the cone, usually on the tree, to emerge the following spring when young cones are developing on Douglas fir.

Several species of parasites were reared from *B. colfaxiana* but the most important was an ichneumonid, *Glypta evetriae* Cush. This species was observed to oviposit in early-instar cone moth larvae. Host larvae completed their development but died immediately after the cocoon was constructed. Most parasites emerged the following spring after overwintering in the host cocoon.

Acknowledgments

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A Technique for Individual Rearing of the Predacious Mite *Melichares dentriticus* (Berlese) (Acarina: Aceosejidae) with Notes on its Life History and Behaviour

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The predacious mite, *Melichares dentriticus* (Berlese), has been mass-cultured (Burnett, 1960) for the past few years at this laboratory on populations of *Tyrophagus putrescentiae* (Schrank) (= *castellanii* (Hirst)) (Acarina: Acaridae) (Robertson, 1959). Individual rearings, however, were required to obtain detailed information on the life history, behaviour, and ecological requirements, prior to the use of this species as an experimental animal in the study of predator-prey interactions. This paper is an account of the various techniques tested and of the observations made throughout these studies.

Rearing Techniques

The primary objective of the work was to develop a suitable technique for obtaining, under controlled temperature and humidity conditions, individual

records on the development of the different stages of the predator as well as accurate data on its fecundity and longevity. Such information could then be used to estimate its rate of increase at any given combination of temperatures and relative humidities. Because of the large number of individual mites usually involved in studies of this kind, the technique must be as simple as possible to keep handling at a minimum. As daily, and sometimes more frequent, observations are necessary, it should also permit easy and rapid examination of the material at any time with a stereomicroscope. With these requirements in mind, a few of the various types of microcells recommended for rearing mites were tested with the different stages of the predator and of the prey.

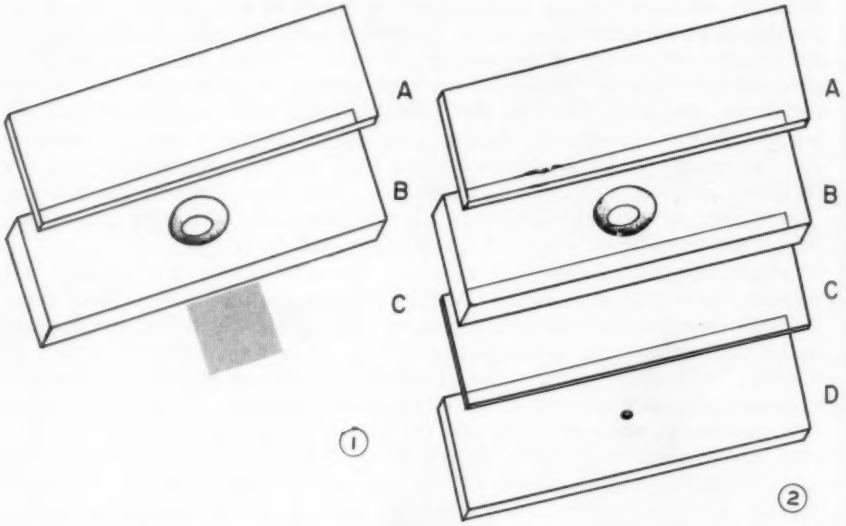
Pharmaceutical capsules, as used by Herbert (1956) for rearing the predacious mite *Typhlodromus* (*T.*) *tiliae* Oudms., are unsuitable. With these the food is usually placed in one portion of the capsule which, when necessary, can be replaced with another one containing fresh food. However, due to difficulties in handling active stages of the prey, only the eggs or the dormant larvae and nymphs can conveniently be fed to the predator. Even then transfer of the predator to a new cell each time the food is changed may also be necessary as the prey are often scattered by the predator. Another objection to the method is that softening of the gelatin capsules at temperatures above 77°F. causes stickiness and opacity, thus interfering with handling of the material and observations of the activities and development of the mites.

The plaster-charcoal technique as modified and later used by Rohde (1956, 1959) for rearing the mite *Caloglyphus mycophagus* (Megnin) and its predator *Fuscuropoda marginata* (Koch) likewise was not suitable. Even smaller cages of this type are rather bulky and only a few can be stacked conveniently into the desiccator jars used as constant-humidity chambers. Also, because of the difficulties involved in handling, frequent cleaning of the rearing chambers or preparation of new ones would become prohibitively time-consuming.

For the sake of simplicity of preparation and handling, rearing cages of the "slide type" were found to be the best under these circumstances. Straight-sided cells, such as hanging-drop slides or cells consisting of a ring cemented to a slide, however, are unsatisfactory because the whole interior can not be readily examined under a microscope and mites wandering on the sides of the chamber are difficult to observe. The cages finally selected were of two kinds depending on the food given to the predator.

When only eggs of the prey are supplied, a cell similar to the type developed by Robertson (1944) is satisfactory (Fig. 1). It consists of a hole in the form of a truncate cone measuring one-half inch at the top and five-sixteenths of an inch at the bottom drilled through the center of a rectangular strip of acrylic plastic (B) about one by three by one-eighth inches. A piece of fine mesh nylon cloth (C) (235 meshes to the linear inch glued to the lower surface of the plastic provides a permeable base to the encised cell. This is enclosed above by an ordinary microscope slide (A) secured to the plastic at each end by means of a strip of paper held in place with a small rubber band. There is no need for a seal of paraffin or petroleum jelly and opening or closing of the cage is therefore greatly facilitated. Prey eggs in sufficient numbers are easily introduced into the rearing chamber if they are first attached with vaseline to a small piece of paper. The eggs are seen most readily if the paper is black.

When active stages of the prey are fed to the predator one must use a cage that provides a constant supply of fresh food to these mites and at the same time will prevent the escape of the minute larvae that are able to squeeze through



Figs. 1 and 2. Disassembled rearing cages. Fig. 1. Cage used for individual rearing of *Melichares dentriticus* on eggs of *Tyrophagus putrescentiae*. A. Microscope slide. B. Plastic strip. C. Nylon cloth. Fig. 2. Cage used for individual rearing of *Melichares dentriticus* on active stages of *Tyrophagus putrescentiae*. A. Microscope slide. B. Plastic strip. C. Cellophane sheet. D. Plastic strip.

very small openings. The microcell selected (Fig. 2) is essentially the same as the one previously developed by Rivard (1958) for experimental rearing of the prey species on mould cultures, except that the rearing chamber is of larger size in order to provide plenty of room for the mites. Parts (A) and (B) are the same as in the cage described above (Fig. 1), but the nylon cloth forming the base of the cell is replaced with a sheet of moist, water-permeable cellophane (C) laid over a second strip of plastic (D) one-sixteenth of an inch thick. A hole about one-sixteenth of an inch in diameter drilled halfway through the centre of this second strip is filled with a paste made of water and powdered wheat germ. The mould that is grown on top of the cellophane in the area covering the wheat germ occupies only a small portion of the cell at its centre, and allows the prey to feed all around it with but a little risk of being entrapped in the mycelium. Enough free space for predator activity is left at the periphery. Though the two plastic slides must fit snugly at the edges of the cell to prevent the mites from escaping or from getting trapped underneath, the rearing chamber is not air-tight and its humidity presumably becomes similar to that of the exterior within a few hours.

Both types of cells are relatively easy to prepare and may be handled with a minimum of trouble. Because of their shape and size, they can be stacked in trays in such a way as to occupy little space, and as many as forty cells have been placed inside a six-inch diameter desiccator jar over a humidity-regulating solution. They can be disassembled, cleaned and re-used indefinitely. They may be examined rapidly at any time with a stereomicroscope. Identification numbers and other necessary data may be written on the strips of paper that are wrapped around both ends of the cages.

Notes on the Biology of *M. dentriticus*

A number of observations were made on the life history and behaviour of *M. dentriticus* while experimenting with the techniques. The cells were placed inside desiccator jars in which the relative humidity was maintained at about 80 per cent by means of an appropriate sulphuric acid solution (Solomon, 1951) and rearing was done in an air-conditioned room at 72 ± 2°F. The cells were kept in semi-darkness during the daytime by slipping heavy paper bags over the jars.

Preliminary tests were conducted on the feeding habits of the adult predators confined in individual cells and supplied with various stages of *T. putrescentiae*. They successfully attacked any stage of their prey within such restricted areas, but deutonymphs and adults were preyed upon only as a last resort and would probably succeed in eluding the predators in a larger environment. Freshly laid eggs were eaten readily but those more than two days old, having a tougher shell, could withstand the attack without suffering damage. The adult predators were also cannibalistic when short of normal food and starving females occasionally were observed to feed upon their own eggs and larvae. The nymphs preferred the younger stages of the prey, whereas the larvae were rather inactive and did not feed.

Apparently *M. dentriticus* searches for its prey at random and does not react positively until an actual contact is made. When a prey is encountered, the predator makes sudden motions, seizes it with its palpi and first pair of legs, and swiftly feels the body of the prey with its chelicerae, apparently searching for a point of entry. Penetration generally occurs through the latero-ventral surface between the first two pairs of legs and is accomplished by pushing with the chelicerae held together as a spear. Then the body fluid of the prey is gradually absorbed until only a shriveled mass is left. The number of individual prey consumed during a given period of time varies greatly according to the size and stage of both the prey and the predator. For instance, *M. dentriticus* must eat an average of 70 eggs, or about 50 young larvae, to complete its development; if mature larvae or protonymphs were supplied instead, this was further reduced to about 30 individuals. It fed sporadically, sometimes eating as many as five or six prey, then waiting half a day or so for the next meal. Egg-laying females were usually more consistent in their feeding and ate as many as ten larvae each day, but developing nymphs had their largest meal soon after moulting and very little nourishment was absorbed at the end of this stage.

In preliminary studies on the development of 50 predators reared individually on eggs of the prey, mortality was practically nil during the egg and larval stages but was over 50 per cent during the nymphal stages. Most of the mortality was probably caused by starvation, the nymphs being unable to pierce the egg shells of the prey. This was confirmed in another tests where each of 25 nymphs reared on larvae of the prey successfully reached the adult stage. The durations of the various stages in both tests were as follows:

Stage of prey	Egg	Larva		
No. predators	13 males	Length of development in days		12 females
		10 females	13 males	
Stage of predator				
Egg	2.0	2.0	2.0	3.0
Larva	1.5	1.5	1.5	1.5
Protonymph	3.5	4.0	2.5	2.5
Deutonymph	4.0	7.5	3.0	3.0
Total	11.0	15.0	9.0	10.0

Observations were made twice a day and the mean figures obtained were rounded to the closest half-unit. Though the average duration of the egg stage was about the same in each instance, there was much variation between the individuals. Apparently the female predator can lay fully developed eggs since sometimes the eggs hatched within a few hours after deposition though in some cases as many as four days of incubation were required. The larval stage, on the other hand, always lasted from one to three days. When the protonymphs were reared on larvae of the prey they completed their development in one and a half to three and a half days, but when reared on eggs they sometimes required up to seven and a half days. The range of variation was still greater for the deutonymphs, especially the females, with a minimum of two and two and a half days respectively and a maximum of five and fourteen days respectively on these diets. The total time required for development was significantly shorter ($P<0.01$) for the mites reared on larvae of the prey than for those reared on eggs, and in both instances the males always developed a little faster than the females.

Time did not permit to carry out a detailed investigation on the fecundity of the predator, but a few pairs were kept under observation for various periods and the records obtained, though incomplete, nevertheless yielded some useful information. Copulation between virgin adults usually occurred within ten minutes after being placed together. The male soon located the female, crawled about her body and eventually took a position under her, both sexes facing in the same direction with their ventral surfaces opposed. As a rule the pair remained in that position for at least half an hour, the female carrying the male with her whenever she moved about. Only the mated females laid eggs, and oviposition began from three to five days after mating. The eggs were usually deposited singly on the slide or on the bare floor of the rearing chamber. They were infrequently found inserted in the mycelium of the mould culture. Females that fed upon eggs of the prey laid only from eight to ten eggs at the rate of one every second or third day, but females that fed on larval prey laid about twice that number during the same period and some individuals occasionally deposited two eggs on the same day. To facilitate handling, the male was removed from the cage the day after mating and the female was kept isolated thereafter until oviposition had ceased for five or six days. If another male was then reintroduced with the female, mating usually was observed again but oviposition resumed in only a few instances. Longevity of the adult females averaged seven to eight weeks, but, exceptionally, one female lived for fifteen weeks.

A few tests were also made with mould as the only source of food for nymphs and adults of the predator. Under these conditions the nymphs died in a few days without moulting and mated females failed to oviposit. Though feeding on mould was not actually observed, adults kept on that diet lived about two weeks but those without any food lived only eight or nine days. These results are not conclusive; however they suggest that the predator cannot develop or reproduce in the absence of prey but can probably survive for a longer period if mould is present than if no food is available.

Summary

A technique is described for rearing individually the predacious mite *Melichares dentriticus* (Berlese) on various stages of *Tyrophagus putrescentiae* (Schrank). The predator apparently searches at random and attacks any stage of its prey. It feeds primarily on the larvae and protonymphs and is occasionally cannibalistic. The number of prey consumed varies with the size and stage of

both the prey and the predator. At a temperature of 72°F. and a relative humidity of 80 per cent, development of the male and of the female was completed in nine and ten days respectively on a diet of prey larvae; these periods lasted eleven and fifteen days respectively when the mites fed upon eggs of the prey. Only the mated females laid eggs, and oviposition began from three to five days after mating. Usually eggs were laid singly at intervals of two or three days, and longevity of the females averaged about seven weeks. The predator cannot develop or reproduce in the absence of prey but will probably survive for a longer period if mould is available than in the absence of any food.

Acknowledgment

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The Interaction of the Spruce Budworm, *Choristoneura fumiferana* (Clem.), and the Parasite *Glypta fumiferanae* (Vier.)[1]

By C. A. Miller[2]

This is the second of a series of papers (Miller, 1959) describing the interaction of primary parasites and the spruce budworm, *Choristoneura fumiferana* (Clem.), based on data collected during an outbreak of the budworm in northern New Brunswick during the period 1947-1958. The first paper showed that the interaction between the spruce budworm and *Apanteles fumiferanae* Vier. is adequately described by the general mathematical model developed by Watt (1959). The data on the parasite *Glypta fumiferanae* (Vier.) to be presented in this paper are also analysed by means of Watt's model and consequently the method is essentially the same. There is, however, one important difference. In the case of *A. fumiferanae*, the estimated number of adult parasites was only an index based on the potential number emerging from the previous host generation. The observed density of *G. fumiferanae* is a more realistic estimate. It is based on the actual number of cocoons found on the foliage during the adult emergence period.

The study of the role of parasites in a spruce budworm outbreak is part of a long-term project, called the Green River Project, which was set up in 1945 to

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investigate the population dynamics of the budworm (see Morris *et al.*, 1958). The study area is located on the Green River Watershed in northwestern New Brunswick. A description of the permanent study plots and the annual population density of first-instar larvae on each has been presented (Miller, 1959, Table I). The *G. fumiferanae* analysis is based on data collected on these plots with the exception of Plot K1-S and N1 for which detailed cumulative defoliation records pertinent to the present analysis are lacking.

Life-History of *Glypta fumiferanae* (Vier.)

G. fumiferanae is a common parasite of the spruce budworm in eastern and western North America (Wilkes *et al.*, 1948; Dowden *et al.*, 1948). A description of the adult and immature stages is given by Brown (1946). In the Green River area it may be considered a specific univoltine parasite since it has not been recorded from other hosts. Its synchronization with the life-history of the budworm is as follows:

Time	*Budworm*	*G. fumiferanae*
Late July to early August	Egg	Adult
Early August	First instar	
Mid-August	First and second instar in hibernaculum	Egg
Late August to mid-May	Second instar in hibernaculum	First instar
Early June	Third instar	First instar
Late June to early July	Sixth instar	Maturing larva
Mid-July to late July	Pupa and adult	Cocoon

Observations on caged adults indicate that *G. fumiferanae* attacks first- and second-instar larvae in hibernacula. Female longevity is approximately 30 days in cages. The parasite overwinters as a first-instar larva and emerges from either fifth- or sixth-instar hosts. Oviposition experiments using both small glass containers and caged trees in the field were not successful in indicating reproductive potential. The maximum number of attacks per female was 143, but this figure is not considered a reliable estimate since the failure of a number of females to oviposit suggests that nutrition or the environment was sub-optimal. In both series of experiments the adults were fed on an aqueous honey solution.

Estimation of Number of Hosts Attacked and Parasite Density

Number of Hosts Attacked.—The number of hosts attacked is the product of second-instar host density and the proportion of hosts parasitized. The second-instar host density is an estimate based on egg counts (less egg mortality) assuming that the fall dispersal loss of larvae from eclosion to the spinning of hibernacula is approximately 64 per cent. This estimated population figure is used because actual counts of second-instar larvae in hibernacula are lacking for many plots, although a reliable sampling technique has been subsequently devised for this stage (Miller, 1958). In any case, the analysis of fall dispersal loss on a number of plots in different years (Miller, 1958) indicates that it is relatively constant (in contrast to spring dispersal loss) and the use of a mean estimate of 64 per cent therefore does not introduce a significant variable in assessing the number of hosts attacked.

Estimates of per cent parasitism by *G. fumiferanae* were obtained by two methods owing to the protracted period during which the parasite is present in the host, and also to the particular methods used in studying the parasite complex of the budworm. Thus, in most instances early-stage larvae were dissected and

TABLE I

Variation in Per Cent Parasitism Based on Two Sampling Methods and Also on Periodic Collections, 1954

Plot	No. of larvae		Per cent parasitism		Seasonal variation in parasitism (Diss.)[1]			
	Reared	Dissected	Rearings	Dissections	Early June	Mid-June	Late June	Early July
G2	181	295	5.0	9.2		−4.2	+3.2	−0.7
G4	291	315	16.8	14.0		+2.7	−0.1	−4.0
G5	191	350	8.4	11.4	−3.4	+0.7		+1.9
G6	111	300	9.9	8.7	+0.5	−0.9		+0.1
G8	340	300	12.6	10.3		−2.3		+2.4
K2	304	510	8.9	6.5	−1.3		+0.5	+3.5

[1]Deviations from mean per cent parasitism calculated from the total number of larvae dissected.

ultimate-instar larvae were reared. Both techniques yield reliable estimates of parasitism as shown in Table I and, in practice, both results are combined to give a single estimate. Tables I and II also show that no consistent deviations exist in per cent parasitism based on periodic collections ranging from second- to sixth-instar larvae. Deviations in estimates of parasitism based on second- and third-instar collections that may have resulted from the dispersal of second-instar larvae (Miller, 1958) did not occur because *G. fumiferanae*, unlike *A. fumiferanae*, shows no differential degree of attack within tree crowns. Dissection of second-instar larvae collected from five trees showed means of 10 per cent parasitism in the top half and 11 per cent in the bottom half of the crowns.

Adult Parasite Density.—The density of *G. fumiferanae* is based on cocoon counts obtained from the same foliage samples that are used for estimating the population of spruce budworm pupae. This ensured a representative sample per plot (Morris, 1955). At low host densities, however, cocoons are scarce and

TABLE II

Comparison of Per Cent Parasitism Based on Second- and Third-Instar Host Collections

Plot	Instar	Larvae examined	Per Cent parasitism
K2	II	109	0
	III	331	0.6
K1	II	156	0.6
	III	177	2.3
K2	II	170	2.4
	III	332	2.1
G12	II	610	2.5
	III	147	4.1
K2	II	620	3.2
	III	200	0.5
K3	II	540	3.7
	III	200	4.0

zero counts may occur in the sample. The following technique was devised to correct for zero counts. The correction is based on the hypothesis that cocoon counts (Pc) are a function of the estimated number of cocoons (Pe) that should occur in a population where host density and proportion of hosts parasitized are known. An analysis of 44 sets of data showed that Pc is a linear function of Pe and that the mean ratio of Pe/Pc = 2.82 ± .28. In the following analysis this ratio was used to obtain calculated Pc values in five cases where zero counts were obtained from foliage samples, and in two cases where no foliage samples were collected on the plot. The standard error of Pe/Pc also indicates that in an analysis of host-parasite interaction, an index of adult parasite density based on host density and the proportion of hosts parasitized in the previous generation may often be reliable when practical difficulties exclude cocoon or actual adult counts.

No precise estimates of cocoon mortality were obtained during this study. One hyperparasite, *Mesochorus sylvarum* Curtis, was recorded on a few occasions.

Analysis

The development of the mathematical model used in the following analysis is discussed in detail by Watt (1959), and its application to field data by Miller (1959). The reader is referred to these papers for a more detailed account of the development of the model and its application.

Definition of symbols:

N_A = number of hosts attacked
N_o = number of hosts vulnerable to attack
P = number of parasites searching
A = coefficient of attack, or the number of hosts attacked per parasite and considered an instantaneous rate
K = maximum number of attacks that can be made per parasite when the hosts are vulnerable
C = cumulative defoliation
a and b = positive constants

The number of hosts attacked expressed in terms of the number of parasites searching and host density is given by the following equation:

$$N_A = PK(1 - e^{-aN_oP^{1-b}}) \quad \ldots\ldots(1)$$

Relationship of N_A to N_o.—Fig. 1 shows the relationship of the number of hosts attacked to host density for three mean parasite densities. The curves are similar to those plotted for *A. fumiferanae* (Miller, 1959) and show that N_A increases at a diminishing rate with an increasing N_o. Holling (1959) also shows similar functional response curves for a wide variety of host-parasite data.

Estimation of K.—The maximum number of attacks capable per parasite (K) is obtained from the following transformation of equation (1):

$$\ln\left(\frac{PK}{PK - N_A}\right) = AN_o \quad \ldots\ldots(2)$$

where P, and consequently aP^{-b}, are held constant. Approximate estimates of K were first obtained graphically and subsequently refined by choosing that value of K which maximizes the correlation coefficient. Table III shows correlation coefficients for the accepted values at three mean parasite densities. K was assumed to equal 70 from these data. This represents, in theory, a reproductive

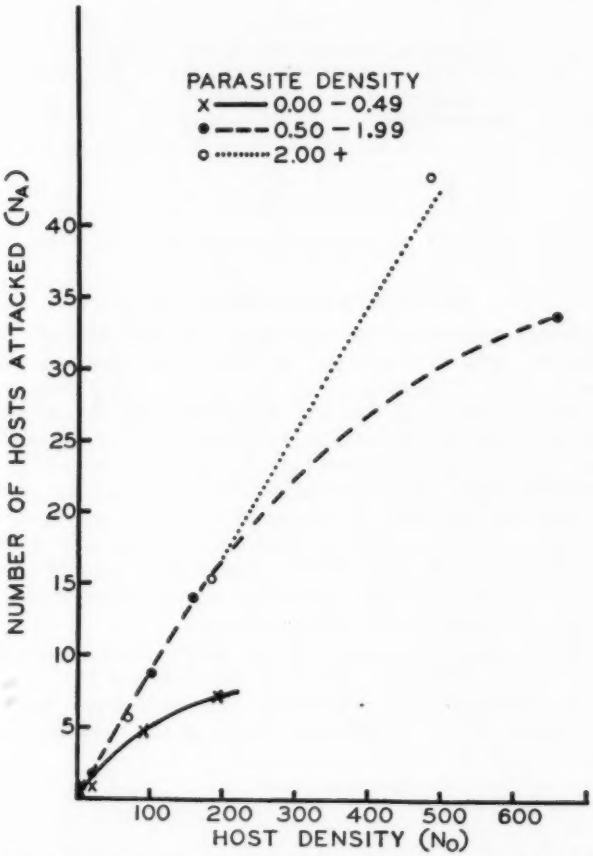

Fig. 1. The relationship of hosts attacked to host density for three densities of *G. fumiferanae*. Plotted points represent group means.

rate of 140 eggs per female (sex ratio 1:1) and approximates the apparent reproductive rate found in oviposition experiments.

Estimation of the Constants a and b.—These constants are obtained from the following transformation of equation (1):

$$\ln\left[\frac{\ln\left(\frac{PK}{PK - N_A}\right)}{N_oP}\right] = \ln a - b \ln P \quad \ldots\ldots(3)$$

with K = 70, this regression analysis yielded a correlation coefficient of — .978 (Fig. 2) and the following values for *a* and *b*:

$$a = .00094$$
$$b = 1.8095$$

Substitution of the above values for K, a, and b, in equation (1) gives the appropriate equation for estimating the number of host attacked.

$$N_{Ac} = 70P(1 - e^{-.00094N_oP^{-.8095}}) \quad \ldots\ldots(4)$$

TABLE III

Estimated K Values at Three Parasite Densities

Mean parasite density	0.16	1.06	4.30
N	19	17	15
K	60	70	70
r	.64	.76	.88

The Effect of Other Factors on N_A

A preliminary plotting of the calculated over the observed values of N_A indicated that N_{Ac} was overestimated on these plots where severe defoliation either caused a marked thinning of the foliage on living trees or ultimately resulted in tree mortality. It was first determined that the deviations in N_{Ac} could not be explained by the relationship of either N_o or P to defoliation and then deduced that the attack efficiency of the parasite is apparently lowered in severely defoliated stands, either because defoliated trees are less attractive to the parasite, or defoliation increases crown exposure to light, which, in turn, affects parasite behaviour. The fact that *G. fumiferanae*, unlike other budworm parasites (Miller, 1953, 1959), does not attack a greater proportion of hosts in the top half of tree crowns may indicate a preference for the more shaded portions of the crown and adds weight to the latter assumption.

Although the causal relationships are not clearly understood, *a* was assumed to be a function of defoliation. The term defoliation as used herein does not refer to current defoliation, but is defined as the yearly accumulation of current defoliation estimates. It is, therefore, an index of the total defoliation history of the stand.

$$a = f(C) \quad \ldots\ldots (5)$$

substituting (5) in (1) gives

$$\frac{\ln\left(\frac{PK}{PK - N_A}\right)}{N_o P^{1-b}} = f(C) \quad \ldots\ldots (6)$$

This regression was first tested graphically using cumulative defoliation and the natural logarithm of cumulative defoliation. The latter gave the line of best fit (Fig. 3).

The equation of this line, with a correlation coefficient of — .94 based on class means, is

$$\frac{\ln\left(\frac{70P}{70P - N_A}\right)}{N_o P^{-.8096}} \times 10^4 = 31.28 - 4.374 \ln C \quad \ldots\ldots (7)$$

$$\text{or } a = .0031 - .00044 \ln C \quad \ldots\ldots (8)$$

Substitution of (8) in (4) gives the modified equation for estimating the number of hosts attacked.

$$N_{A_c} = 70P[1 - e^{-(.0031 - .00044 \ln C) N_o P^{-.8096}}] \quad \ldots\ldots (9)$$

The calculated number of hosts attacked by *G. fumiferanae* was obtained from equation (9). A comparison of observed and calculated values by means

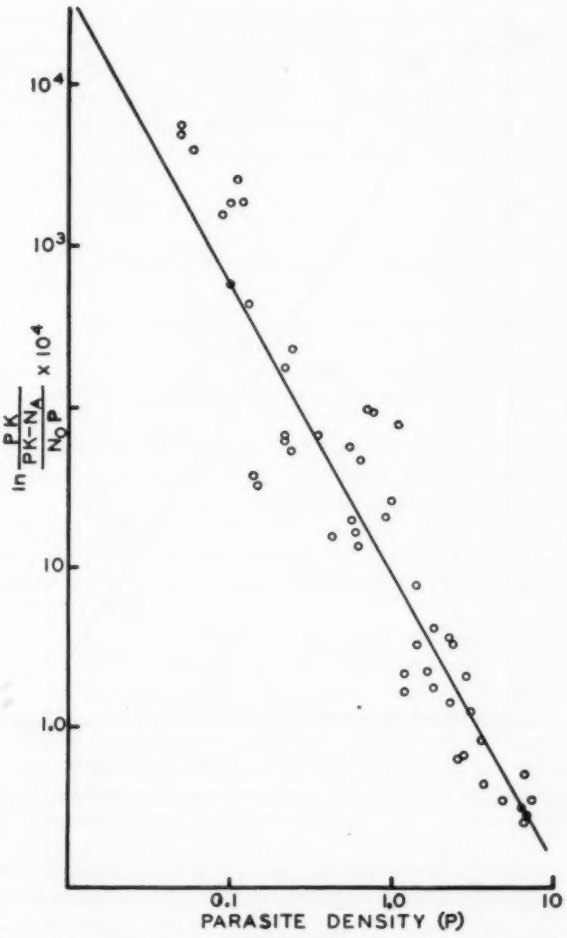

Fig. 2. Test of equation 3 to evaluate searching by *G. fumiferanae* for second-instar budworm. See text for definition of symbols.

of a regression analysis showed that the equation explained 78 per cent of the variation in N_A, which is an increase of 5 per cent over that explained by equation (4). This compares favourably with the results for *A. fumiferanae* where the model explained 71 per cent of the variation in N_A.

Attempts to find other factors that may have had a significant effect on the number of hosts attacked were carried out graphically by plotting the ratio of N_{Ao}/N_{Ac} over values of these factors. Particular attention was paid to weather including cloud cover, precipitation, and temperature. Mean annual estimates of these factors for the period when *G. fumiferanae* were active showed no significant relationship. An analysis of precipitation did indicate that in years of heavy precipitation, particularly 1954, the calculated number of hosts attacked was higher than observed values, suggesting that heavy precipitation hinders parasite attack. However, since only eight values for rainfall were available, and seven of these had a narrow range, it was not possible to show significant effects.

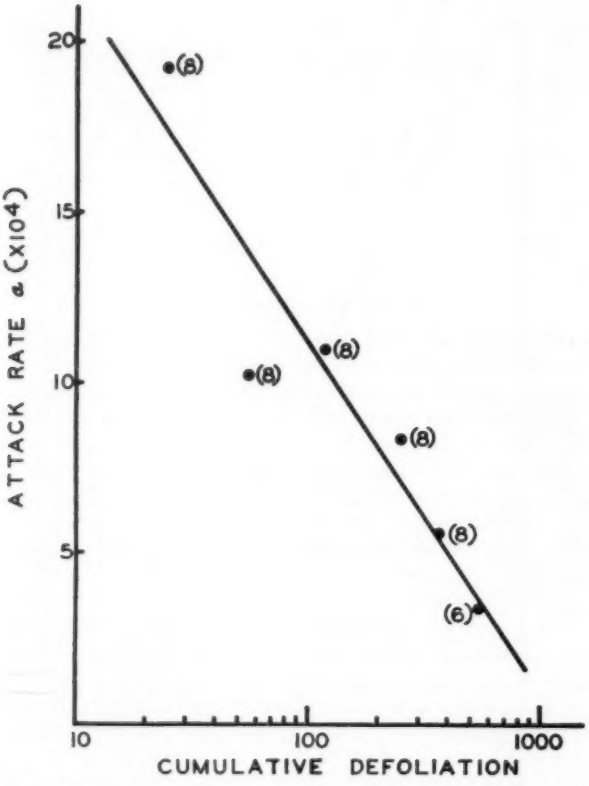

Fig. 3. Graph showing the effect of cumulative defoliation on the attack rate of *G. fumiferanae*.

Stand factors including the number of trees per acre, average diameter at breast height, and density were also investigated but none showed a relationship to N_A.

Discussion

The presentation of two equations that mimic the interactions of the spruce budworm and the parasites, *A. fumiferanae* (Miller, 1959) and *G. fumiferanae*, provides an opportunity to evaluate the practical aspects of the results obtained from this type of mathematical analysis. An important contribution is that the numerical values of the parameters in the equation will provide hypotheses for further research into the precise meaning of these parameters in terms of parasite behaviour. A more immediate result, although somewhat unexpected, is that both equations show a decrease in parasite efficiency in a severe infestation. Two dissimilar trends in budworm density occurred on the permanent study plots in the area. In one group, a severe infestation resulted in varying degrees of tree mortality, while on the remaining plots, which were partially isolated by cutting operations, the infestation only reached an intermediate level with little or no effect on the host tree. Both infestations declined to the endemic level at about the same time. Data from these two groups of plots showed that the number of hosts attacked by both *A. fumiferanae* and *G. fumiferanae* was less than expected on plots within the severe infestation area.

No direct cause and effect relationship was found to explain the decrease in parasite efficiency. In the case of *A. fumiferanae*, the decrease was related indirectly to parasite survival (Miller, 1959), while the present analysis shows that defoliation is related to the attack rate of *G. fumiferanae*. In order to show how the latter could affect the trend in host density, a hypothetical example showing the interaction between the spruce budworm and *G. fumiferanae* has been calculated from equation (1).

$$N_A = PK(1 - e^{-aN_0P^{1-b}})$$

Estimates of N_0 and P for successive generations were obtained by substitution of the following values:

$N_0 = 10$
$P = .35$ } (First generation values taken from field data.)

$K = 70$

$a = .0031$ (Value of *a* in the absence of defoliation from equation (8).)

$b = 1.8095$

F = rate of increase of the budworm = 3. (This represents the effective rate of increase from year to year in the absence of moth invasion.)

D = rate of increase of the parasite. It was assumed that no mortality factor acted on the parasite. Thus, the number of hosts attacked in one generation (N_A) equals the parasite density P of the following generation. In practice, field data indicate an average survival of *G. fumiferanae* from egg to cocoon of 16 per cent.

The calculations showed a sharp increase in N_0 followed by a similar trend in P. A peak density was reached in the ninth generation and, at a level of approximately 65 per cent parasitism, N_0 began to oscillate about a mean density as shown in Fig. 4B. The effect of defoliation on the attack rate of *G. fumiferanae* may be seen by comparing Figs. 4A and 4B, where both trends in N_0 start from an initial population of 516. In Fig. 4A, where it is assumed that 100 per cent current defoliation occurs in successive years, N_0 increases 15-fold over the next three generations, while Fig. 4B shows N_0 oscillating about a mean density of 545 in the absence of defoliation. This example is clearly exaggerated because of a very high parasite density but it does serve to illustrate how *G. fumiferanae* would fail to regulate a rapidly rising budworm population which reaches a level causing severe defoliation.

Fig. 4B is of further interest since it shows that Watt's (1959) general model can generate a predator-prey interaction with regular oscillations rather than oscillations of increasing amplitude as predicted by Nicholson's theory (1933). Varley and Gradwell (1958) and Voûte (1958), in a discussion of host-parasite relationships on the basis of the Nicholson theory, show the necessity for a density-related factor to damp oscillations in order to "eliminate the contradiction between the Nicholson theory and observations in nature" (Voûte, 1958). However, as pointed out by Watt (1959), the Nicholson and Bailey model does not provide for a limited attack rate, which is evident in most functional response curves for parasites (Holling, 1959). This question, although of fundamental importance in many studies of population regulation, still awaits a critical analysis. Recent experimental evidence on the nature and form of oscillations in a host-parasite interaction (Utida, 1957; Burnett, 1958) shows conflicting results that are confounded by the time and spatial arrangements of the experimental universe and by changes in the "properties" of host and parasite themselves that arise from methods of propagation (Burnett, 1958).

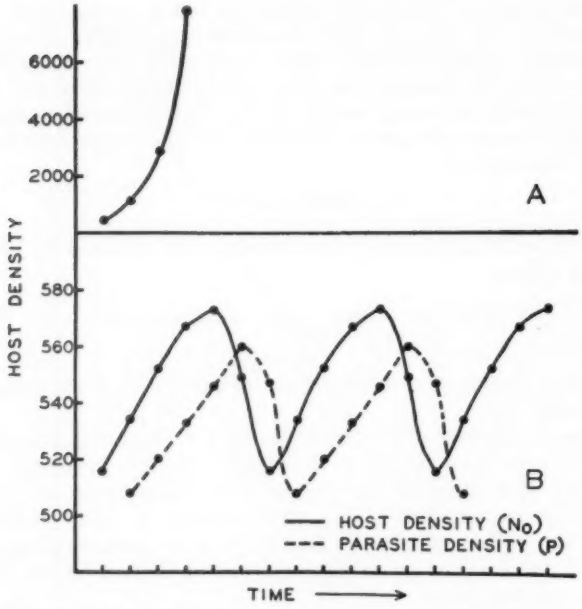

Fig. 4. Two hypothetical budworm population trends, as derived from equations (1) and (9). See text. A. Rapidly rising host population when defoliation causes a reduction in the attack rate of *G. fumiferanae*. B. Regular oscillations of host and parasite in the absence of a defoliation effect on the attack rate of *G. fumiferanae*.

The presentation of Watt's general model (1959) has been followed by an equation describing predator-prey interaction published by Holling (1959). The two models were developed in quite different ways and with basically different objectives. Watt's model is based on a set of reasonable biological assumptions regarding the action of predator and prey at varying densities and has been tested with both experimental and field data. Holling's equation is based on those parts of the functional response, searching, and 'handling' of hosts that are present whenever a predator attacks. These parameters were independently measured in a series of artificial experiments and incorporated into a basic functional response equation. Holling (1959) contrasts the applicability of the two models by comparing the variance explained by each for a series of published data on host-parasite interaction. His equation gave a better fit for nine of 13 comparisons. However, both authors[3] agree that the two models may be considered incorrect in the sense that they are incomplete. Holling's equation probably overestimates N_A as N_A approaches PK. This can be noted in his analysis (1959, Table III, and Figs. 4-6) which invariably shows that his equation gives a better fit where the last point (observed number of hosts attacked) is above the line, and Watt's equation works best where the last point falls below the line. It is evident therefore that a combination of the two models might be needed to give a good fit over a wide range of values.

Table IV shows an analysis of the field data for *G. fumiferanae* based on mean values of N_o and N_A in order to compare the two models. The data were

[3]Holling (1959): Dr. Watt, personal communication.

TABLE IV

Comparison of Descriptive Values of
Holling and Watt Models, Based on Mean Values of N_o and N_A for *G. fumiferanae*

P	N_A	Holling N_{A_c} (1)	Watt[1] N_{A_c} (2)	Sums of squares of deviations (1)	Sums of squares of deviations (2)	Holling's equation
0.16	.07 .58 .77 4.84 7.41	.18 .37 .78 4.16 8.82	.18 .37 .78 3.52 6.17	2.51	3.34	$N_A = .0457\ N_o$
1.06	1.71 8.87 14.0 33.6	1.96 8.35 12.5 35.8	1.45 6.13 9.96 33.2	7.42	24.1	$N_A = \frac{.0912\ N_o}{1 + .00103\ N_o}$
4.32	5.6 15.4 43.4	5.5 14.4 37.3	5.9 15.7 39.3	38.2	17.0	$N_A = .0770\ N_o$

[1]Equation (4).

also sub-divided on the basis of P since Holling's equation does not provide for a variable P. The Table shows that Holling's equation gives a better fit to the data at two of the three parasite densities. However, at P values of 0.16 and 4.32 the 'handling' time, or b, is not significantly different from zero and the equation is reduced to a straight line which states that the number of hosts attacked increases linearly with N_o:

$$N_A = T_t\, a\, N_o$$

where, T_t = total time that hosts are vulnerable to attack
a = a constant termed the instantaneous rate of discovery.

A further example of a host-parasite interaction where the 'handling' time is not significantly different from zero is contained in data cited by Burnett (1958), where 20 *Encarsia formosa* Gahan searched for a varying number of hosts equally distributed over a 25-square-inch plane during an 18-hour period. Burnett states that "the percentage of hosts parasitized . . . . was approximately equal". Under these conditions Holling's equation becomes a straight line. Although a straight line fully describes the experimental results for *E. formosa* and part of the field data for *G. fumiferanae*, it fails to predict the expected trend in either host-parasite interaction. In both cases N_A would approach an upper asymptote rather than increase linearly with N_o. For example, Burnett (1958) states that the fecundity of *E. formosa* probably lies between four and eight eggs per female and, with P = 20, N_A would approach an upper asymptote at values ranging between 80 and 160.

Watt's model, as well as giving a good fit to the *E. formosa* data, also predicts that N would approach an upper asymptote. The transformation equation (2) gives a PK value of 120. Thus, since P = 20, K = 6. The computed value of K therefore approximates the biological value and, in this instance, does not warrant the criticisms cited by Holling (1959).

Conclusions

The analysis of field data obtained during an outbreak of the spruce budworm in northwestern New Brunswick shows that the effect of the primary parasite, *G. fumiferanae*, is described by Watt's (1959) model of predator-prey interaction and adds further support to its general application in describing field data (Miller, 1959). The refined model for *G. fumiferanae* contains a modification to express the effect of defoliation on the attack coefficient. The analysis also suggests that extremes in weather conditions may lessen the attack efficiency of the parasite.

Acknowledgments

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(Received March 10, 1960)

Lecanium coryli L. (Homoptera: Coccoidea) in Saskatchewan[1]

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Richards (9) recognized five species of *Lecanium* for Canada – namely *L. coryli* L., *L. cerasifex* Fitch, *L. tiliae* L., *L. nigrofasciatum* Pergande and *L. caryae* Fitch. *L. coryli* L. and *L. cerasifex* Fitch were distributed from British Columbia to Nova Scotia; *L. tiliae* L. occurred only in British Columbia. Further, Richards (9) drew the following conclusions:

1.) *L. coryli* is the *L. corni* Bouché of Marchal (1908) and of most European workers but is not the *L. corni* of North American workers.

2.) *L. corni* Bouché of Sanders (1909) and subsequent North American workers is a mixture of two species, *L. corni* Bouché of Marchal and *L. cerasifex* Fitch of Richards.

3.) *L. tiliae* is *L. coryli* of Marchal (1908) and subsequent workers.

According to Glendenning (5) *L.* (*Eulecanium*) *coryli* L. was introduced into British Columbia from England in 1903 and by 1923 was causing serious damage to maple and horse chestnut and was present also on many other woody plants. Since no mention is made of other species of *Lecanium* it appears possible that *L.* (*Eulecanium*) *coryli* reported by Glendenning (5) and later investigated by Graham and Prebble (6), included a mixture of species subsequently known to occur on Vancouver Island and the mainland and to be present on various plant hosts. McLeod (8) adds support to this view. It is also probable, because of the coast-to-coast occurrence of *L. coryli* and *L. cerasifex* in Canada, that reports of *L. corni* (4) occurrence, particularly in areas of the United States bordering on southern Canada, have inadvertently included *L. coryli* and *L. cerasifex* as recognized by Richards. The use of the term '*corni* complex' in some of the more recent reports indicates that a mixing of identities may exist. Further, it is possible that *L. cerasifex* as designated by Richards, being present in Ontario on the east and British Columbia on the west, occurs also in the Prairie Provinces.

Plants listed as hosts of *L. coryli* in Canada are alder, apple, apricot, beech, birch, caragana, elm, hawthorn, horse chestnut, laurel, lime, maple, pear, plum, poplar, raspberry, rose and willow (5, 9).

Lecanium scales have been important chiefly as orchard pests, and in the absence of parasites have increased to alarming numbers, requiring the adoption of applied control. Miscible oils and oil emulsions have given good control when applied as dormant sprays in the fall and early spring (3, 7), and the gun-type application produced better results than mist application (3). High paraffinic type oils were more effective than napthenic types of oils (10). Asquith (2) found that by spraying with DDT and BHC to control general pests in orchards, the abundance of *L. corni* Bouché was increased, where formerly this scale had been kept in check by parasites.

Since *L. coryli* was the only species reported for a Prairie Province (9), it is assumed by the writer that previous *Lecanium* records for the prairie region pertained to *L. coryli*. These records show that *L. coryli* has been present on shelterbelt and shade trees for many years but until recently was not sufficiently abundant in any locality to constitute a pest. In 1943 it was found at Bow Island, Alberta, and at Alameda, Bradwell, Colonsay and Plunkett, Saskatchewan.

[1]Contribution No. 6, Forest Nursery Station, Research Branch, Canada Department of Agriculture, Indian Head, Saskatchewan.

It was discovered at Caron, Saskatchewan, in 1944, and at Edgerton, Alberta, in 1946. By 1950 it was moderately abundant at Indian Head, Saskatchewan, and noticeably present on park and boulevard trees at Regina, Saskatchewan. This increase was the beginning of a marked buildup in the *L. coryli* population. By 1957 severe infestations occurred at Indian Head, Regina and Moose Jaw, Saskatchewan. The foliage of infested elm trees was thin and the twigs and branches were coated with honey dew and black fungus. The severe condition continued in 1958, but by the end of the 1959 season a marked decline had taken place.

The following account is a summary of investigations of *L. coryli* on American elm, carried out at Indian Head and Regina, Saskatchewan, in 1957, 1958 and 1959.

Development and Seasonal Activities

L. coryli occurred on American elm, *Ulmus americana* L., green ash, *Fraxinus pennsylvanica* Marsh. var. *lanceolata* (Borkh.) Sarg., boxelder, *Acer negundo* L., and caragana, *Caragana arborescens* Lam., the host preferrence being in the order given. American elm in both urban and rural areas was heavily infested whereas populations on caragana were sporadic and very light. Only one annual generation of the scale was noted.

The scale overwintered as immature nymphs, which were most frequently to be found under scaly bark and in crevices on the mid and upper trunk and the proximal portion of the main branches. The nymphs were often congregated in masses several insects in depth. Nymphs also hibernated on the smooth bark of the terminal parts of the branches. The relative distribution of such nymphs, as indicated by the number of insects per 12-inch length of branch growth, was as follows:

Current year, one-year, two-year growth	0 nymphs
Three-year growth	14 nymphs
Four-year growth	60 nymphs
Five-year growth	110 nymphs
Six-year growth	66 nymphs
Seven-year growth	55 nymphs

Many of the nymphs which hibernated on the terminal parts of the branches occurred under dead females of the previous generation. Seventeen per cent were so located in a sample examined April 11, 1958. Often, where dead females occurred in groups, several hibernating nymphs would be present under one individual with none occurring under the remaining females in the group. The frequency of this mass association indicated that it was not due entirely to chance. Very few nymphs hibernated in close proximity to dormant buds, and none on dead branches.

Emergence of the nymphs from hibernation occurred from late March to the second week in May. Nymphs were active on April 4 in 1957, and emergence began about April 1 in 1958 and 1959. Table I presents data on emergence for 1958 and 1959. The 1958 data represent emergence on the basal portion of large elm branches and were obtained by suspending short branch sections in the mid crown of a large tree and recording, at intervals, the nymphs which became trapped on bands encircling the upper ends of the sections. The bands were white adhesive tape, one inch in width and coated with tanglefoot. The 1959 data were obtained by placing similar tanglefoot bands at the 20-foot level, around main branches of an elm tree, and recording the nymphs trapped on them.

TABLE I
Emergence of *Lecanium coryli* L. Nymphs in 1958 and 1959

Date	1958		1959	
	(No.)[1]	(%)[2]	(No.)[1]	(%)[2]
April 2	80	0.8		
6	1868	19.1	97	4.0
8	1151	30.4	1	4.1
10	34	30.7	2	4.2
14	2505	55.3	27	5.3
16	627	61.4	254	15.8
17	84	62.2	224	25.1
21	1096	73.0	946	64.4
23	457	77.4	376	80.0
27	76	78.2	32	81.3
30	137	79.5	73	84.4
May 4	546	84.9	346	99.0
7	1054	93.2	11	99.2
9	488	100.0	20	100.0
Totals	10203		2409	

[1]Number of nymphs trapped since preceding observation
[2]Accumulated percentage of the total for year

Emergence activity of the nymphs appeared to be directly related to atmospheric temperatures. Nymphs were always more numerous and activity greater on the side of the tree trunk exposed to the sun. Nymphs were observed to be inactive on days when the maximum atmospheric temperature was below 39°F and the daily mean was less than 33°F. They were very active on days when the maximum atmospheric temperature approached 60°F and the daily mean was above 40°F. Table I shows that emergence was generally less during the first three weeks in April in 1959 than in the same period in 1958. The temperature during this period was lower in 1959 than in 1958. Fifty per cent of the emergence in 1958 was accomplished before April 14; it was achieved several days later in 1959. Emergence terminated about May 9 in both years.

The nymphs which survived hibernation and spring migration settled on the twigs and the terminal portion of the branches. Their abundance on such growth varied greatly from tree to tree and year to year. The number per 12-inch twig averaged approximately 120 nymphs on heavily infested elm trees in the Regina area in 1957, less than 60 in 1958 and less than 10 in 1959. In the Indian Head area the density was approximately 110 nymphs per 12-inch twig in 1958, and very much less in 1959. Average densities on elm in the district of Vancouver, British Columbia, ranged from one to 233 nymphs per 12-inch twig during the period 1942 to 1945 (6). The upper limit of this range was considered extremely high. It was almost twice as great as the highest density recorded for the Regina area.

Many nymphs had matured by May 15. Oviposition had begun by late May and was concluded by late June or early July. Two types of gravid females, which differed somewhat in external appearance, were noted. These occurred together on the same twigs. One type consisted of large individuals, hemispherical in shape and mottled-brown in colour. The second-type females were smaller, somewhat elongated and flattened, grey and slug-like in appearance. The amount of sticky exudate voided by the smaller females was greater than by the larger ones, and oviposition was less.

TABLE II
Mortality of *Lecanium coryli* L. Nymphs in Hibernation on Exposed Portion of Elm Branches

Location	Total Nymphs	Dead
	(No.)	(%)
Regina (Urban)	355	95.4
Regina (Rural)	6570	72.2
Indian Head	9946	71.8

Data on the occurrence and development of males were not obtained. Consequently, the influence of male abundance on oviposition was not ascertained. Graham and Prebble (6) found that 19 to 34 per cent of the adult females failed to oviposit and attributed this failure to lack of fertilization caused by insufficient males. The percentage of fully-developed females which had not begun ovipositing by the fourth week in June in 1959 ranged from 7 to 12 per cent at Indian Head, and 3 to 17 per cent at Regina, indicating that the percentages of females fertilized were relatively high.

Hatching began in late June and continued throughout July. Less than one week after hatching commenced the new generation of nymphs began to appear on the foliage. The nymphs showed a marked preference for the lower surface of the leaves where 76 per cent of the recorded insects occurred. The nymphs also exhibited a marked tendency to settle close to the midrib and larger veins. Nymphal populations occurring on the foliage were quite variable. They ranged from several hundred nymphs per leaf on severely-infested elms, in 1957 and 1958, to less than 100 nymphs per leaf, in 1959 in the same areas.

The migration from the foliage back to the branches and trunk for hibernation began in late August. In 1958, bands of white adhesive tape and coated with tanglefoot were placed around branches in the upper crowns of elm trees in the Regina area to investigate the progress of this movement. The bands were examined daily to count the nymphs trapped on them. Nymphs began to appear on the bands on August 22 and continued until November 4. The total number of insects trapped on 10 bands during this period was 221,923. Fifty per cent of the nymphs had reached the bands by September 9, 75 per cent by September 15 and 90 per cent by September 20.

Natural Mortality

Physical Factors

Weather is probably the most important factor complex influencing population density of *L. coryli* in the Prairie Provinces. The marked, and frequent changes in temperature, relative humidity and precipitation affected every active stage of the insect. The greatest mortality occurred during winter dormancy.

Approximately 67 per cent of the nymphs, which hibernated under scaly bark and in crevices on the trunk and main branches of elm trees in the fall of 1957, were dead by the spring of 1958. Higher mortalities occurred where hibernation took place in more exposed sites. Table II shows the loss in the spring of 1959 of nymphs which hibernated on the smaller branches of elm trees.

The losses of nymphs which survived hibernation and migrated to the twigs and smaller branches during the spring of 1959 are summarized in Table III. Many of the nymphs succumbed before they were well established on the twigs and branches. Only a small percentage died after they were full-grown.

TABLE III
Mortality of *Lecanium coryli* L. Nymphs
after Emergence from Hibernation

Location	Total Nymphs	Dead
	(No.)	(%)
Regina (Urban)	17129	35.8
Regina (Rural)	8289	31.1
Indian Head	2170	23.9

Mortality of nymphs during the leaf-inhabiting phase was quite variable. Table IV presents data for infestations on elm in 1958. Additional undetermined losses occurred through dislodgement of nymphs during the feeding period, and the failure of nymphs to vacate the foliage before the leaves were shed in autumn.

Underdevelopment

Some nymphs which survived hibernation remained alive on the twigs and branches during much of the season but in a retarded stage of development. These did not lay eggs and, therefore, represented a loss of scale population. The percentages recorded on elm for Regina (Rural) and Indian Head, in 1959, were 17 per cent and nine per cent respectively. The phenomenon of retarded growth was observed also by Graham and Prebble (6) on Vancouver Island and on the British Columbia mainland. The percentage of underdeveloped nymphs varied from year to year and from place to place. It varied also from host species to host species. The causes of underdevelopment were not determined by Graham and Prebble but evidence suggested that year, locality and host were important factors.

Parasitism

Parasitism of the adult female scales was investigated in 1958 and 1959. Table V shows the incidence of parasitized females in the samples examined. Although variable, the amount of parasitism tended to increase from 1958 to 1959. In 1958, it was highest in the Regina (Urban) area where *L. coryli* had been the most numerous in 1957. From 12 to 50 per cent of the females parasitized in 1959 laid some to many eggs. Twelve species of parasites were obtained and a report on them will be prepared at a later date.

Applied Control

In the present investigation, infested elm trees were sprayed with summer-type, high-volume sprays which were applied at 350 p.s.i. One set of sprays was applied April 14 when approximately 50 per cent of the overwintered

TABLE IV
Mortality of *Lecanium coryli* L. Nymphs
During the Leaf-Inhabiting Period

Location	Date	Total Nymphs	Dead
		(No.)	(%)
Regina (Urban)	July 23	556	17.6
	July 29	334	37.1
Regina (Rural)	Aug. 8	8486	5.4
	Aug. 20	18172	19.2
Indian Head	Aug. 1	4077	4.1

TABLE V

Parasitism of *Lecanium coryli* L. Females in 1958 and 1959

Location	1958		1959	
	Females	Parasitism	Females	Parasitism
	(No.)	(%)	(No.)	(%)
Regina (Urban)	9449	43.0	—	—
Regina (Rural)	2152	5.2	719	10.4
Indian Head	2170	18.5	2674	42.6

nymphs had emerged and reached the twigs and branches. A few leaf buds were bursting on the host trees. The second lot was applied May 16 after the migrated nymphs had become established on the twigs and branches. The third, fourth and fifth were foliar treatments and were applied July 18, August 8 and August 19, respectively. Table VI gives the insecticides and concentrations used for each lot and the mortality effected by each treatment. The relatively low mortalities in the checks for lots 1 and 2, Table VI, resulted from the samples being drawn from the twigs and smaller branches, thus eliminating a high percentage of mortality associated with hibernation. The results presented in Table VI show that the summer-type sprays were not satisfactory for controlling the nymphal stages occurring on the trunks and branches, and that lime sulphur was ineffective as a foliar treatment. Effective control of *L. coryli* is indicated, however, for malathion and diazanon emulsions applied as foliar treatments.

TABLE VI

Insecticidal Treatments and Control of *Lecanium coryli* L. Achieved

Spray Lot	Insecticide Formulation	Rate Applied[1]	Insects Treated	Total Mortality	Kill Achieved[2]
			(No.)	(%)	(%)
1	Malathion 50% E.	2 qt.	2692	83.6	73.6
	Malathion 50% E. and Oil[3]	2 qt.	4735	68.1	48.7
	Self-Emulsifying Oil[3]	2 gal.	8858	47.0	14.8
	Mulsicut Oil[4]	1 gal.	2700	46.4	13.8
	Check - water		18881	37.8	
2	Diazanon 25% E.	2 qt.	713	51.1	21.9
	Malathion 50% E.	2 qt.	644	37.4	2.9
	Check - water		7600	35.8	
3	Malathion 50% E.	2 qt.	3480	93.5	91.4
	Malathion 50% E.	1 qt.	3629	87.3	85.5
	Dry Lime Sulphur	8.3 lb.	5545	18.3	6.9
	Check- water		4220	12.2	
4	Diazanon 25% E.	2 qt.	15539	90.4	88.9
	Malathion 50% E.	2 qt.	12438	89.0	87.3
	Check - water		20557	13.5	
5	Malathion 50% E.	2 qt.	1377	97.8	94.7
	Malathion 50% E.	1 qt.	1097	89.9	75.6
	Dry Lime Sulphur	8.3 lb.	994	27.2	0.0
	Check - water		1688	58.5	

[1]Amount in 100 gallons of water
[2]Calculated (1)
[3]Two gallons summer-type oil - N. M. Bartlett Mfg. Co. Ltd., Beamsville, Ontario.
[4]Light, miscible petroleum oil - British American Oil Co., Regina, Saskatchewan

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Summary

An outbreak of *Lecanium coryli* L. on American elm in the Indian Head and Regina areas of Saskatchewan was investigated during 1957 and 1959. Data were obtained on seasonal occurrence, development and habits, natural mortality, and applied control experiments were conducted. The nymphs hibernated on the trunks and branches, and spring emergence occurred from April 1 to May 9. Some females had begun egg-laying by late May. Hatching started in late June and new-generation nymphs appeared on the foliage by early July. Migration from the leaves to the branches and trunks occurred from late August to early November. Mortality percentages attributed to physical factors were, 67 per cent for nymphs in hibernation on the trunks, 70 per cent for nymphs in hibernation on the terminal parts of the branches, up to 35 per cent for nymphs which survived hibernation, up to 37 per cent for new-generation nymphs on the leaves. A small segment of the population persisted as underdeveloped nymphs. Several species of parasites were reared from adult female scales and the percentages of parasitism ranged from five to 43 per cent. Summer-type sprays were ineffective against the spring and early summer stages. Malathion and diazanon were effective against the stages on the leaves.

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The Importance of the European Pine Shoot Moth, *Rhyacionia buoliana* (Schiff.) in Quebec City and Vicinity[1]

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Introduction

Although the European pine shoot moth is well known as a pest of pines where winters are moderate, particularly in southern Ontario (1, 2, 3, 6), its occurrence in the Province of Quebec has been sporadic and confined chiefly to the more southern regions. There have been occasional reports of this insect in Montreal since 1931 and in Grand' Mère since 1934, but it was not until 1954 that it was discovered in Quebec City. Since that time, however, it has been recorded from several other localities. In 1958, it was found in a nursery at Sayabec, in the Matapedia Valley.

Following its initial discovery in Quebec City, a survey of the immediate vicinity revealed that the infestation was not more than three to four years old and limited to small areas. The insect was mainly restricted to the small ornamental pines, but the infestation was sufficiently severe to warrant an investigation of the principal factors of natural control affecting all stages.

Materials and Methods

R. buoliana was found almost exclusively on Mugho pine, *Pinus mugo* Turra, and for this reason collections were later restricted to this tree species. Because of its small size the Mugho pine afforded a good chance of survival to the overwintering stage of the insect and it was also the most common pine species found in gardens and parks around the city.

Collections were taken on trees ranging from one to seven feet in height and the number of shoots collected on each tree varied from three to ten depending on its size. Sampling was done from late May to the middle of June, in order to obtain both larval and pupal stages.

The material collected was reared in the laboratory in lots of about 30 shoots in one-gallon "Sealright" containers. Each of these was fitted with a glass tube for the capture of adult insects, and the emergence was recorded daily. The method proved quite satisfactory since 92 per cent of the insect material was reared to maturity.

Similar collections were made in February or March. Shoots collected at that time were kept at room temperature for 36 to 48 hours and then dissected for larval recovery. The number of living and dead larvae as well as the number of sound and damaged buds, were recorded.

Results

Parasitism

Parasitism of *R. buoliana* has continuously increased since 1954 (Table I). No parasites were recovered from the material collected in 1954 at the time of discovery but parasitism reached 66.2 per cent five years later. A similar increase in parasitism occurred throughout all the areas sampled. On the other hand, larval populations of *R. buoliana* decreased almost as steadily in all areas except Ste. Foy near Quebec, where sampling showed an increase owing to extensive planting of infested ornamental pines.

The parasite species on *R. buoliana* in this part of Quebec are largely identical with those found in Ontario (8), but the percentage of parasitism is

[1]Contribution No. 633, Forest Biology Division, Research Branch, Department of Agriculture, Ottawa, Canada.

TABLE I

Rearing results obtained from late larval and pupal collections of *Rhyacionia buoliana* (Schiff.) made in and around Quebec City from 1955 to 1959 inclusively, on Mugho pines

Localities	Years	Number of larvae & pupae collected	Number of moths emerged	Number of parasites emerged	Percentage of parasitism
Quebec (West)	1955	17	13	3	16.8
	1956	273	116	82	41.4
	1957	20	2	17	89.4
	1958	12	2	10	83.3
	1959	62	21	40	65.5
Sillery (Centre)	1955	524	410	68	14.2
	1956	198	135	43	24.1
	1957	132	44	78	69.3
	1958	21	14	7	33.3
	1959	30	6	24	80.0
Sillery (West)	1955	343	318	2	.6
	1956	234	192	15	7.2
	1957	382	263	77	22.6
	1958	198	152	46	23.2
	1959	164	65	94	59.1
Ste. Foy	1955	5	5	0	.0
	1956	33	29	2	6.2
	1957	66	47	8	14.5
	1958	17	13	4	23.5
	1959	83	19	60	75.9
Totals	1955	889	746	73	8.9
	1956	738	472	142	23.1
	1957	600	356	180	33.5
	1958	248	181	67	27.0
	1959	339	111	218	66.2

much higher. This is due almost entirely to *Orgilus obscurator* (Nees) which for some reason is more effective. During the last three years this species alone was responsible for more than 85 per cent of the total parasitism of the host (Table II). *Orgilus obscurator* is of European origin, but as far as is known it has never been released in this province.

A few collections made in the cities of Sherbrooke, Granby, and Montreal during the summer 1956 showed that the effectiveness of *O. obscurator* was general throughout these areas. An interesting hyperparasite, *Perilampus fulvicornis fulvicornis* Ashm., was recovered for the first time on *O. obscurator* in 1959. It was found in a collection from a nursery in the City of Ste. Foy and sent to this laboratory by the Quebec office of the Plant Protection Division.

Another parasite of European origin, *Temelucha interruptor* (Grav.), was recovered for the first time in 1958 at Sayabec, in the Matapedia Valley, and at Sillery, west of Quebec City. Incidentally this species gained more importance during 1959, mostly in the latter locality.

Apart from the species mentioned above, only two other important hymenopterous parasites were found during the five years of survey; 16 specimens of *Horogenes* sp. were reared in 1955 and 38 of *Itoplectis conquisitor* (Say) in 1956, but they were never found in such numbers during subsequent years.

Winter mortality of the larval stage

Although some American authors have already investigated winter mortality of *R. buoliana* in areas where lethal temperatures (—18° F.) prevail, their studies

TABLE II

Parasite species recovered from late larval and pupal rearings of *Rhyacionia buoliana* (Schiff.) collected in Quebec City and vicinity from 1955 to 1959 inclusive

Species	Number recovered per year				
	1955	1956	1957	1958	1959
Orgilus obscurator (Nees)	56	86	163	61	180
Horogenes sp.	16	–	1	–	–
Itoplectis conquisitor (Say)	–	38	3	3	–
Itoplectis evetriae Vier.	–	8	1	–	–
Calliephialtes comstockii (Cress.)	–	5	–	–	1
Scambus pterophori (Ashm.)	–	2	–	–	–
Scambus hispae (Harr.)	1	2	–	–	–
Scambus sp.	–	1	5	–	8
Campoplex sp.	–	–	–	–	3
Temelucha interruptor (Grav.)	–	–	–	2	25
Ichneumonidae sp.	–	–	7	1	1
	73	142	180	67	218

were almost always concerned with the insect in natural stands and plantations of red and Scotch pine. (1, 2, 4, 6, 7, 9)

In the areas studied in Quebec, Mugho pines are usually kept at hedge height (one to six feet), so that they are usually covered by snow most of the winter. This, coupled with the fact that Quebec City is one of the most northern localities where *R. buoliana* is known to exist in Canada, provided some interesting observations on the effect of climate on the hibernating larvae.

The timing of the snow cover is probably the key factor controlling larval winter mortality. For example, the winter of 1955-56 presented the most unfavourable conditions for larval survival. In December 1955, the larvae were exposed to lethal temperatures for approximately six consecutive days before the first snowfall. On the other hand, the winter 1957-58 (Table III) presented the most favourable conditions for survival in the four years of winter records.

TABLE III

Mortality of overwintering larvae of *Rhyacionia buoliana* caused by lethal temperature, compared with minimum temperatures and snowfall during the months of December and January in Quebec City from 1952 to 1959 inclusively.

Years	Conditions of temperature and snowfall					Number of shoots sampled	Number of larvae found	Per cent mortality
	Snowfall (in inches)			Min. Temp. °F.				
	Dec.	Jan.	Total	Dec.	Jan.			
1952–53	24	25	49	− 7	−16			
1953–54	13	30	43	9	−33			
1954–55	42	13	55	7	−17			
1955–56*	21	14	35	−18	−19	131	315	84
1956–57*	10	17	27	−16	−29	158	121	96
1957–58	42	32	74	2	−23	79	21	33
1958–59	29	23	52	−14	−12	158	87	50

*Unfavourable years.

Protection for the larvae resulted from an unusually heavy snowfall early in December 1957 accompanied by relatively high temperatures in the same period.

Although no data on populations are available prior to 1955, the climatic conditions help to explain the high population levels encountered (Table III). In 1955 the average count was 1.3 larvae per infested shoot, but it was not uncommon to find as many as five larvae in one shoot.

After two adverse winters, 1955-56 and 1956-57, average population counts showed .27 larvae per infested shoot, and in the spring 1959, after two favourable winters, it was up again to .90 larvae per infested shoot.

The normal severe winter climate prevailing in the Quebec City area is apparently prejudicial to the successful establishment of this insect. Almost every year during December and January lethal or sub-lethal temperatures are recorded for many days. This confirms the opinions expressed by Benjamin, Smith, and Backman (2), that in zones "where lethal temperature occurs 4 to 5 times every five years the shoot moth should have little opportunity to become established."

The degree of winter mortality may reach between 50 and 100 per cent during adverse winters and continuity of an infestation is dependent on the survival of larvae in small pines well covered by snow early in the winter.

Conclusions

An investigation of the European pine shoot moth and its factors of biological control over a period of five years in the Quebec City area showed that more than 60 per cent of the larvae of *R. buoliana* were parasitized. A braconid of European origin, *Orgilus obscurator* (Nees), is mostly responsible for this situation. This parasite is now well established and more effective than in other parts of the country where parasitism seldom rises over 12 per cent.

As in most of its northern range in North America, this insect is also killed by severe cold, and when the snowfall is light, or occurs late in the season, very high larval mortality is registered. In Ontario and in the northern States it is not uncommon to find 65 to 85 per cent larval winter mortality. In Quebec, during the winter season all larvae above snow level are killed, thus ensuring good protection for the pine trees in plantations and only small ornamental pines in gardens and nurseries have been infested.

These observations suggest that the European pine shoot moth has very little chance of becoming economically important in the Province of Quebec.

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Observations on the Spread of *Cyzenis albicans* (Fall.) (Tachinidae: Diptera), an Introduced Parasite of the Winter Moth, *Operophtera brumata* (L.), (Geometridae: Lepidoptera), in Nova Scotia[1]

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Cyzenis albicans (Fall.) has been introduced into Nova Scotia as a control measure against the winter moth, *Operophtera brumata* (L.). The parasite attacks the late larval stages of the winter moth, pupates within the host in the ground, and emerges in the spring. The first liberations were made at Oak Hill near Bridgewater and the dates of releases as well as the numbers released were reported by Graham (1958) as follows: 1954, 31; 1955, 1008; 1956, 1005; 1957, 250. Graham made recoveries of *C. albicans* from rearings of larvae collected at Oak Hill in 1956 and 1957 and found that parasitism was less than two per cent both years. While liberations have been made at other locations in the Province since 1957, no further releases have been made at or near Oak Hill.

Since 1957, the winter moth has been the subject of an intensive population study by personnel of the Forest Biology Sublaboratory at Debert, Nova Scotia, particularly after 1958 when a study area of approximately 1100 acres was established at Oak Hill. In addition to Plot 1-2 (actually a combination of two plots) which had been in existence there since 1953 and was in the immediate vicinity of the liberation points, a series of eight plots was set up, distributed throughout the study area in two roughly parallel lines, with the farthermost plot being 1.2 miles from Plot 1-2.

To measure changes in larval population, permanent sample trees, five in Plot 1-2 and three in each of the remaining plots, were sampled by the method devised by Morris and Reeks (1954). Samples were taken at three- to seven-day intervals throughout the larval feeding period and the larvae collected were reared in battery jars. These rearings provided a check on parasite development and the degree of parasitism. The determination of percentage parasitism was based on pupal rearings, with the assumption that larvae dying during the rearing procedure were parasitized to the same extent as the larvae that survived to pupate. All parasite determinations were checked by the Entomology Research Institute, Ottawa.

In 1958, parasitism by *C. albicans* had increased to nine per cent in Plot 1-2, the release site. More important, the parasite had been recovered from Plot 3 which was one-half mile from Plot 1-2 and separated from it by a stand of conifers as well as a cut-over area, both containing relatively few winter moth host trees. Parasitism in Plot 3 was three per cent.

[1]Contribution No. 637, Forest Biology Division, Research Branch, Department of Agriculture, Ottawa, Canada.

TABLE I

Summary of Winter Moth Parasite Studies at Oak Hill, N. S., 1959

Plot No.	Per cent parasitism	Miles from liberation point	No. larvae reared	No. pupae survived	Host intensity (larvae per leaf cluster)
1-2	24	0	197	148	1.6
5	19	0.6	232	89	3.2
6	17	0.9	32	30	0.4
3	10	0.5	119	102	1.6
10	8	0.8	77	75	1.1
7	5	1.1	29	21	0.4
8	4	1.2	31	25	0.4
9	4	1.0	75	57	1.1

In 1959, parasitism by *C. albicans* (Table I) was 24 per cent in Plot 1-2, 10 per cent in Plot 3, and the parasite had spread through all the remaining plots (except Plot 4) to the farthermost plot, which was one mile from the liberation site. Parasitism ranged from four to 19 per cent in the newly infested plots. The absence of the parasite in Plot 4 was probably due to the small collections of larvae that were made in this area as the result of the low host density that existed there.

Because of the increase in parasitism in Plot 1-2 during 1958, and to serve as a complementary method of assessing parasitism, dissections were made of mature larvae collected in the plot the following year. This method did not give accurate results because of the difficulty in detecting the parasite larva, which does not develop beyond the first instar until after the host pupates. Parasitism based on dissections of 340 larvae was 7.9 per cent.

The dissections gave an indication of the degree of superparasitism and 18.5 per cent of the larvae parasitized by *C. albicans* contained more than one *C. albicans* larva. Multiparasitism was also evident with a nematode (poss. *Complexomermis* sp.) being found in 22 per cent of the larvae that were also parasitized by *C. albicans*.

According to the distances between plots (Table I), *C. albicans* spread at least one-half mile from Plot 3 in 1959. This is equal to the distance of spread in 1958 and suggests that the rate of movement of *C. albicans* in infested areas, once it has become established, is about one-half mile per year. Regarding the increase in the degree of parasitism, it appears that host density has not yet become an important factor and that, so far, percentage parasitism in any particular area has been more dependent on the distance of the area from the liberation site. This can be shown by comparing the distances from the liberation site with percentage parasitism per plot. The negative correlation between the two factors is significant at the five per cent level. On the other hand when host densities are compared with percentage parasitism per plot, there is no correlation.

Plot 1-2 is of considerable interest since the parasite has been established there for at least three years. The degree of parasitism has been increasing each year and the host density in this area may soon be expected to limit the degree of parasitism. However, host density during 1959 was approximately one-quarter that of 1958, yet the increase in percentage parasitism was more than two-fold, suggesting that percentage parasitism may not yet have reached its peak. The significance of this is that according to Varley (1956) in his work on *C. albicans*

in England, the highest percentage parasitism by all species of parasites found in the winter moth population was 30 per cent and this occurred when host density was high. Varley also found that the parasite could not control the host at low host densities because of the behaviour patterns of the parasite, heavy mortality to parasite pupae in the ground, and perhaps synchronization difficulties. However, in view of the degree of parasitism already reached in Plot 1-2, where the host density has been only moderately high (average defoliation has not been higher than 54 per cent since 1955), *C. albicans* may possibly be more successful here than in England.

Through the continuation of the life-table studies it should be possible to demonstrate the influence of this new factor, *C. albicans*, on the population behaviour of the winter moth in Nova Scotia. These tables show that population density before the establishment of the parasite has fluctuated considerably from year to year, in direct response to changes in the mortality rate of the first-instar larvae; and that this mortality rate depends on the degree of synchronization between the hatching of the eggs and the bud bursting of the host trees. Since the larvae cannot feed on closed buds, survival depends on the proportion that reaches the foliage after the buds are open. When synchronization is unfavourable to the insect most of the larvae die and the population does not reach the point where competition for food occurs in the later instars. But when synchronization is favourable, mortality from food shortage becomes high. Thus, in the absence of effective natural enemies, population fluctuations have been largely a matter of chance (spring phenology) with food supply as the density-dependent factor which determines the upper limits. On theoretical grounds, various speculations could be made as to the possible effects of the parasite on this type of population behaviour. It is hoped that the continuation of the life-table studies, which will now be expanded to include survival data on *C. albicans*, will reveal these effects in a quantitative way.

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A New Species of *Pityophthorus* Eichhoff (Coleoptera: Scolytidae) from Alberta[1]

By G. R. Hopping[2]

Swaine (1918) recognized 31 species of *Pityophthorus*. Subsequently 91 new species have been described (Blackman 1920, 1921, 1922a, 1922b, 1928; Swaine 1925; Schedl 1930, 1931) making a total of 122. Some have been transferred to other genera, and others have been placed in synonymy (Blackman 1928; Wood 1957) leaving 115 species now recognized. The following description of a new species was prepared after examination of 50 species of *Pityophthorus*, including examples from the U.S. National Museum, the Canadian National Collection, and Forest Biology Laboratories across Canada. The loan of this material is greatly appreciated. No species have been described previously from alpine larch, *Larix lyallii* Parl. The description is based on examination at a magnification of 50 times.

Pityophthorus alpinensis, new species

Holotype, female: Length 2.78 mm. (front margin of pronotum to tip of elytra), width 1.03 mm. (mid-way between base and tip of elytra); body black, shining.

Head with the front plano-concave from eye to eye, without a carina, densely and moderately finely punctate, somewhat rugose, with the flattened area margined with a fringe of incurved, yellow-grey setae approximately 0.24 mm. in length, with shorter grey setae on the central portion; antenna dark brown, 0.42 mm. long, with club 0.15 mm. long and appreciably longer than the funicle, the club broadly oval in outline, 1.2 times longer than wide, the first segment distinctly narrower than any other, the third segment the widest, the first and second together shorter than the third and fourth together, the first suture rather feebly arcuate, the second and third sutures progressively more strongly arcuate; eye coarsely granulate, the emargination deep and narrow.

Pronotum 1.03 mm. long, 0.89 mm. wide; with posterior margin feebly sinuate, the posterior angles rounded; with a slight constriction at a point two-thirds from the base to apex, the sides feebly and evenly arcuate behind this; anterior margin evenly rounded, with well developed sub-acute serrations which become larger towards the centre; asperities in irregular, roughly concentric rows extending approximately to the middle of the disk; summit moderately elevated, rather weakly impressed behind it and with an impunctate, median strip extending from the summit to the posterior margin; on either side of this strip the posterior areas of the pronotum coarsely and closely punctate, the diameter of each puncture usually greater than the distance between adjacent punctures.

Elytra 1.75 mm. long, 1.03 mm. wide, with the sides feebly arcuate, evenly rounded behind; striae scarcely impressed, the strial punctures moderately coarse and close together, separated by about the diameter of a puncture, in regular rows; interstrial punctures very sparse, nearly as large as strial punctures; the punctures at the base of the elytra more numerous and confused; ninth interspace definitely elevated; declivity gradual, sulcus shallow, moderately wide, shining, the punctures of first stria obsolete, the second strial punctures evident but greatly reduced, sutural elevations each with a row of small granules, lateral elevations low, each with a row of small granules.

1 Contribution No. 666, Forest Biology Division, Department of Agriculture, Ottawa, Canada.
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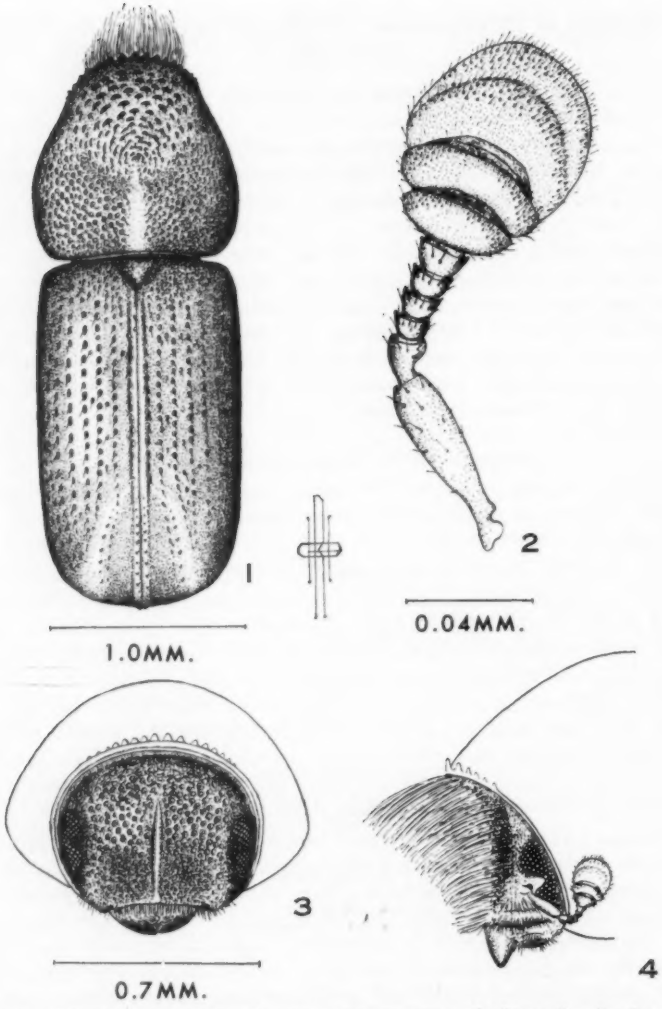

Figs. 1-4. *Pityophthorus alpinensis* n.sp. 1, pronotum and elytra, female; 2, antenna of female; 3, front of head, male; 4, side of head, female.

Ventral surface rather coarsely punctate, with decumbent short grey setae; tip of the abdomen with longer grey setae.

Allotype, male: Similar to the female in size, colour, and punctation, except the front of the head which is coarsely and closely punctate-rugose, feebly convex, with sparse, short grey setae and a fringe of longer grey setae along the margin of the epistoma; front with a median, longitudinal carina extending from the front margin to a point even with the posterior margins of the eyes, the area on either side of the carina slightly impressed on the lower part.

Holotype, female: Canada, Department of Agriculture, Forest Insect Survey No. "56 - A - 913 - 01, Reared 24 - IX - '56 (Sept. 24, 1956), Highwood Pass, Alta., A. larch" (Latitude 50°35′ N., Longitude 115°00′ W.), No. 7291 in the

Canadian National Collection. *Allotype, male*: same data as holotype. *Paratypes*: 8 males, 8 females, same data as holotype; 2 males, Survey No. "58A - 1202 - 01, Sunshine Ski Lodge, Banff, Alta., Em. 3 - IX - '58;" 1 female, same data as above except, "Em. 5 - IX - '58," in the Canadian National Collection; 4 males, 4 females, "56 - A - 912 - 01, Reared 24 - IX - 56, Highwood Pass, Alta., A. larch," in the United States National Museum; 4 males, 4 females, same data as holotype except females have Survey No. "56 - A - 912 - 01," in the California Academy of Sciences, San Francisco; 4 males, 4 females, "56 - A - 912 - 01, Em. 6 - VI - '57, Highwood Pass, Alta., A. larch," in the collection of the University of British Columbia; 2 males, 2 females, same data as holotype except Survey No. "56 - A - 912 - 01" for males, and for 1 female, "Em. 10 - IX - '57," in the Forest Insect Survey Collection, Forest Biology Laboratory, Calgary.

This species belongs in Group I of Blackman (1928) because of the characters of the antenna and the elevated ninth interspace of the elytra. It appears to be more closely related to *P. scalptor* Blackm. than to any other but it differs in the following characters: It is consistently larger (2.68 mm. in length compared to 2.46 mm. for *scalptor*), darker in colour, with the base of the elytra not appreciably wider than the pronotum and the punctures on the posterior areas of the pronotum much coarser. The front is less impressed below in the male than in *scalptor*, which is said to breed in several species of pine in California (Blackman 1928).

Specimens of *P. alpinensis* are quite uniform in size, 10 males picked at random ranging in length from 2.45 mm. to 2.75 mm. (ave. 2.68 mm.) and 10 females varying in length from 2.51 mm. to 2.78 mm. (ave. 2.71 mm.). A few males have the frontal carina interrupted in the middle and in one or two specimens the carina is obsolete. Besides the type series, 112 specimens have been examined from the following localities: Highwood Pass (elevation 7,230 feet), reared from a broken top of alpine larch, collector C. E. Brown; Sunshine Ski Lodge (elevation 6500 feet) near Banff; and above Temple Ski Lodge (elevation 6600 feet) near Lake Louise, from alpine larch, collector N. W. Wilkinson. The species is probably distributed throughout the range of alpine larch which occurs at elevations between 6000 and 7500 feet in the Rocky Mountains from the headwaters of the North Saskatchewan River southward into Montana. It should also be sought in the alpine larch stands of the Selkirk and Cascade Mountains.

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(Received July 6, 1960)

Establishment of *Bombus* spp. (Hymenoptera: Apidae) in Artificial Domiciles in Southern Alberta[1]

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Since Fye and Medler (1954) described methods of obtaining establishment of bumble bee queens in artificial domiciles in Wisconsin, we have been obtaining colonies for pollination and food-preference studies by similar means. The following is a summary of our experiences with the Fye-Medler type of above-ground domicile. Most of the trials were conducted in the prairie region of southern Alberta with grassland species of bumble bees; one was conducted in the foothills of the Rocky Mountains in southern Alberta, where species peculiar to treed areas are common. Because bumble bee queens make their nests in deserted mice nests, domiciles with entrance holes 1¼ inches in diameter were partly filled with roughed-up flax straw and set out in the fall to first provide homes for mice. The following spring, the mice were expelled and mice-excluders (thin metal plates 2 inches square, with holes ⅝ inch in diameter) were nailed over the original holes (cf. Fye and Medler, 1954).

Modifications to Fye-Medler Procedures

Because the mice often lined their flax-straw nests with wool or grass, and because upholsterers' cotton was easier to handle than flax straw and was readily accepted as a nest-building material by mice and bumble bees, upholsterers' cotton was used instead of flax straw. Domiciles were no longer put out in the fall when it was found that bumble bees colonized domiciles that had not been previously occupied by mice. As the mice-excluders did not exclude the white-footed mouse, *Peromyscus* sp., new domiciles of ¾-inch plywood with entrance holes ⅝-inch in diameter were made (Fig. 1). There was no evidence of mouse activity in any of the 500 domiciles like this used in 1959, suggesting that a hole through ¾-inch wood acts as a *Peromyscus*-excluder whereas the same-sized hole in a thin metal plate does not. Fye and Medler (1954) occasionally found mice in their boxes and suggested that an entrance diameter of ½ inch would probably solve the mouse problem.

Species That Accepted Domiciles

All of the grassland species in southern Alberta, *Bombus nevadensis* Cress., *B. fervidus* (F.), *B. borealis* Kby., *B. huntii* Greene, *B. rufocinctus* Cress., and *B. rufocinctus*, var. *albertensis* Ckll., and two woodland species, *B. occidentalis* Greene and *B. appositus* Cress., colonized our domiciles. Fye and Medler (1954) obtained colonies of two other species, *B. separatus* Cress. and *B. vagans* F. Sm., in above-ground boxes; *B. vagans*, a common species in Alberta woodland, also accepted one of their subterranean metal containers. *B. rufocinctus*, which is the latest-emerging species of *Bombus* on the prairie, was one of the two species most commonly found in above-ground domiciles here and in Wisconsin. It is unfortunate that this bee is of little use as a pollinator of red clover or alfalfa (Hobbs, Nummi, and Virostek, in press). However, Fye and Medler (1954) obtained many acceptances by *B. fervidus*, *B. borealis*, and *B. vagans* and we by *B. fervidus*, *B. borealis*, and *B. nevadensis*, all of which are pollinators of red clover in Alberta (Hobbs, Nummi, and Virostek, in press). Fye and Medler did not obtain acceptance by the alfalfa pollinator *B. terricola* Kby.; we obtained

[1]Contribution from the Entomology Section.
[2]Entomologist, [3]Assistant Technician.

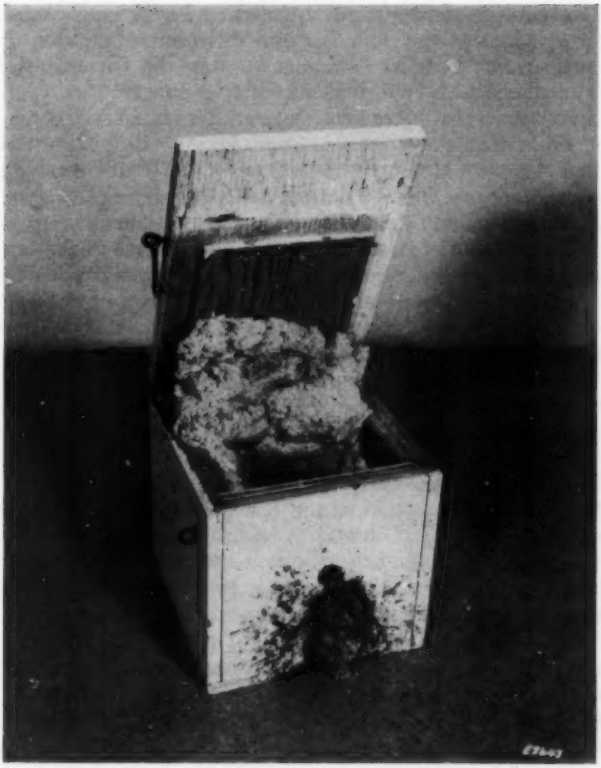

Fig. 1. A domicile of the type used in 1959 in which a colony of *B. huntii* developed.

the acceptance of only one of *B. occidentalis*, a close relative of *B. terricola* and also a pollinator of alfalfa (Bohart, 1957; Hobbs, Nummi, and Virostek, in press). The three most important bumble bee pollinators of alfalfa in Alberta, *B. terricola*, *B. occidentalis*, and *B. ternarius* Say (Hobbs, Nummi, and Virostek, in press), apparently prefer to nest underground (Bohart, 1957; Fye and Medler, 1954), and might accept below-ground artificial domiciles.

The sites of domiciles greatly influenced the number of acceptances. Best results were obtained in fallow backyard gardens, beside fence posts on prairie (*Stipa-Bouteloua* association), and along copses of trembling aspen, *Populus tremuloides* Michx. Over 10 per cent of the domiciles placed in the above sites were accepted. For example, in 1955, seven of 70 domiciles placed beside fence posts along an isolated experimental field of alfalfa on the prairie were accepted whereas none of 30 in brome grass, *Bromus inermis* Leyss., along a shelter belt on a farmstead in an irrigated area were accepted. In 1959, six of 50 placed beside fences surrounding backyard gardens were accepted whereas only two of 60 placed beside fence posts along alfalfa plots in a field of brome grass were accepted. Ten of 74 domiciles along copses of trembling aspen in meadows in the bush country were accepted whereas none were obtained from 50 beside an irrigated experimental field on the prairie.

The results from domiciles in the irrigated area were poor probably because the brome grass obscured the domiciles and their entrances; also, spiders often denied entrance to the bees by spinning webs in the entrance holes. There were so many spiders in the irrigated area that entrances were webbed again a few days after the webs had been removed and the spiders killed.

Enemies of the Bumble Bees in the Domiciles

The worst enemy of the bumble bees in our domiciles was the skunk, *Mephitis mephitis* Schreber. One night in July, 1955, skunks destroyed all seven colonies near an alfalfa field and a nearby colony in a natural subterranean habitat. Though they were not able to remove the lids from two of the domiciles, they were primarily responsible for the destruction of these two colonies also; after the domiciles were righted, harvester ants, probably *Pogonomyrmex occidentalis occidentalis* (Cress.), apparently attracted by the spilled honey, raided the nests and destroyed them. Wiring the domiciles to posts or trees has since prevented skunks from gaining entry, although they tried to do so by digging beneath the domiciles. The excavations were so extensive that the domiciles would have toppled over if they had been weighted down with rocks instead of being tied to posts. Harvester ants have not attacked our nests since.

In 1959, a queen of *B. appositus* and one of *B. fervidus* were destroyed by *Physocephala texana* (Will.) (Diptera: Conopidae), an internal abdominal parasite. Two workers of *B. rufocinctus* were also parasitized by this fly. All were found dead in the domiciles. The queen of *B. appositus* died before her first brood had emerged; then the thief ant, *Solenopsis molesta* (Say) (Hymenoptera: Formicidae), chewed holes in the cocoons. Though the ants were apparently interested only in the detritus within the cocoons and did not attack the pupae, all of the pupae died after the ants had been removed. The queen of *B. fervidus* died after her first brood had emerged; this colony slowly died out but was not attacked by ants.

The queen of *B. occidentalis* was destroyed by *Psithyrus suckleyi* (Greene) (Hymenoptera: Apidae) sometime before July 6, 1959. This queen, which had begun to build her nest sometime before June 12, had time to rear a second brood before she was killed by *P. suckleyi*. Queen supersedure had apparently taken place twice in this nest, as we also found a dead queen of *P. suckleyi* in the nest. The total of about 47 workers produced by *B. occidentalis*, as judged by the number of cocoons in the nest, raised three females and 10 males of *P. suckleyi*.

Neither the bumble bee wax moth, *Vitula edmandsae* (Packard) (Lepidoptera: Pyralidae), nor the mite *Tyrolichus* sp. appeared to harm the bumble bee colonies. In 1959, five colonies were infested with wax moths, but the larvae did not seem to thrive until brood-rearing was completed. The number of brood reared was no greater in the moth-free domiciles than in those with the moth. An infested colony of *B. rufocinctus* produced 242 cocoons whereas the best production of a moth-free colony was 157. All of the above domiciles were being used for the first time and were originally free of the moth. Perhaps the moth would have been a more serious pest if initial infestation had been earlier. Two moth- and mite-free colonies of *B. huntii* produced 121 and 208 cocoons whereas one infested with mites produced 197 cocoons. No damage could be attributed to the mites; Sladen (1912) thought they were harmless and lived on the detritus.

Effects of Moving Colonies

The moving of colonies from the place of acceptance to the crop to be pollinated involved a number of problems. A few of each small first brood were

lost, though entrances were not sealed until after dark, apparently because some foragers remained on the flowers overnight. Free (1955) found that 22.5 per cent of the foragers of a slow-foraging species failed to return to their nests for the night. A few foragers were probably lost at the new site; Free (1955a) found that eight per cent of the foragers were lost when the domicile was moved beyond the foraging area of the bees, apparently because some bees failed to orient themselves when they first foraged from the new site. Queens often foraged after the colonies were moved; all foraged for nectar only. Perhaps this atypical behaviour was a result of having lost some of the foraging workers. As a result of the moving, queens destroyed queens; two of the queens of *B. rufocinctus* apparently returned to the wrong nests soon after the colonies were moved though the domiciles had been tied to posts two rods apart. In both cases a queen was destroyed. In one case, a queen of *B. rufocinctus* was killed by one of *B. rufocinctus*, var. *albertensis*, but no brood of *albertensis* was reared by this colony. Perhaps the destruction of queens in this manner could have been avoided if each of the domiciles had been painted one of the four colours recognized by bees (Frisch, 1950) and had been placed so that no two domiciles of the same colour were next to each other. Fewer queens were produced by colonies that were moved than by colonies that were not moved. Whereas the number of queen cocoons ranged from zero to nine (average four) among colonies of *B. rufocinctus* that had been moved, the range among colonies of this species that had not been moved because establishment was late was 17 to 27 (average 22). Hence, moving of the colonies decreased the chances of survival of the queen, probably slowed down colony build-up, and drastically reduced the number of queens produced during the season.

Summary

It was unnecessary to put domiciles out for occupancy by mice during the winter in order to have bumble bees accept the domiciles the following spring. Upholsterers' cotton, an easily manipulated material, was readily accepted by bumble bees. Apparently a ⅜-inch entrance hole in ¾-inch wood was small enough to exclude the white-footed mouse.

The following species colonized above-ground domiciles: *B. nevadensis*, *B. borealis*, *B. fervidus*, *B. huntii*, *B. rufocinctus*, *B. occidentalis*, and *B. appositus*. These include the important pollinators of red clover in southern Alberta; however, the important pollinators of alfalfa apparently prefer to nest below ground. The percentages of acceptances were greater where the land was fallow or the grass short, indicating that it is better to select sites where the natural nesting habitat is limited and where the bee can easily see the domicile.

Tying the domicile to a post or a tree protected the brood from skunks, the major predators of bumble bees in the region. Other important enemies were *Physocephala texana* and *Psithyrus suckleyi*.

When colonies were moved after the first broods had begun to forage, portions of the first broods were lost; queens apparently had to forage again, thereby decreasing their chances of survival, and some foraging queens entered the wrong domiciles and fought to the death with the rightful occupants. The queen-rearing potentials of colonies that were moved were drastically reduced, apparently as a result of having lost portions of their first broods.

Acknowledgments

We wish to thank N. D. Holmes, C. E. Lilly, and K. R. Depner of the Lethbridge Station for criticism of the manuscript.

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(Received June 9, 1960)

A New Species of *Bracon* from the Pine Root Collar Weevil[1]

By R. D. Shenefelt and I. Millers[2]

During the course of investigations of the life history of the pine root collar weevil, *Hylobius radicis* Buchanan, in Wisconsin, a larval parasite was encountered by the junior author. The Braconid adults which emerged represent an undescribed species of the genus *Bracon.*

Bracon radicis Shenefelt, new species

Runs to couplet 34 in Muesebeck's 1925[3] key but will not fit either alternative since the transverse diameter of the opening between clypeus and mandibles is much greater than distance to the eye and the malar space is as long as the first flagellar segment.

Holotype ♀. Length 3.8 mm., excluding ovipositor; abdomen 1.8 mm.; ovipositor sheaths projecting 2.0 mm.

Head:—Transverse, greatest width 65[4]; length (from lower edge of antennal fossa to occipital carina when viewed at right angle to side of head) 48; depth from vertex to base of mandible 55; distance across mouth opening 30, from mouth opening to eye 10; depth of face from lower edge of antennal fossae to upper margin of clypeus 14; width of face across lower margins of antennal fossae 41; temple of equal width with eye when the head is viewed from the side; eyes scarcely protruding from the contour of the head; ocell-ocular line 4.0 times and the postocellar line 1.75 times the greatest diameter of a lateral ocellus; clypeus protruding, arched to the extent that the anterior tentorial pits appear to be at its sides, narrow, five times as wide as deep; base of mandible 1.5 times as broad as length of malar space. Head smooth and polished except for very minute coriaceous pattern on frons above the antennae, immediately below them and over the area of the malar groove. Face most bulging just below insertion of antennae. Temple bare, center of face bare, scattered pale yellow hairs on sides of face and above eye. Six hairs on ocellar plate, two

[1]Supported in part by the Wisconsin Conservation Department. Approved for publication by the Director of the Wisconsin Agricultural Experiment Station.

[2]Professor and Research Assistant respectively, Dept. of Entomology, College of Agriculture, University of Wisconsin, Madison 6, Wis. The description of the species is to be credited to the senior author.

[3]Muesebeck, C. F. W. 1925. A Revision of the Parasitic Wasps of the Genus *Microbracon* Occurring in America North of Mexico. Proc. U.S. Nat. Mus. 68 (2580): 1-85.

[4]77.5 = 1 mm. in the measurements given in the description.

between the posterior ocelli, one on the mid-point of each lateral ocellar line and two located within the ocellar triangle. Longest hairs on clypeus twice as long as the longest of those adjacent to eye. Antenna with 24 flagellar segments. Length of scape 13, scape compressed laterally, the apex ovoid; pedicel length 8; first four flagellar segments 9, 8, 7, 6; the third and succeeding flagellar segments at least as long as broad, excepting the last three.

Thorax:—Mesoscutum smooth and polished, the notauli weakly impressed and sparsely hairy; propodeum evenly doubly convex, with a central carina at apex extending forward 0.33 of the length of the propodeum, smooth excepting the roughened apical 0.25; lateral portions of pronotum smooth excepting the crenulated furrow and a few very fine aciculations just in front of the furrow; mesopleurae polished; metapleurae smooth, roughened adjacent to posterior coxae. Width across mesonotum at anterior edges of tegulae 63; length of mesonotum 57 (viewed directly from above); scutellum 25 long, 25 wide at base; prescutellar groove narrow (length 4), regularly crenulated, crossed by nine quite regularly spaced ridges.

Legs:—

Anterior:—Coxa-globose, length 17, trochanter segments — (measured on lower side) 13 and 7; femur — length 45, width 13; tibia — length 45, spur 12; tarsal segments — 15, 10, 7, 6, 10; claws simple.

Middle:—Coxa — ovoid, length 23; trochanter segments — 17 and 7; femur — length 45, width 13; tibia — length 55, inner spur 9; tarsal segments — 14, 9, 8, 5, 10.

Hind:—Coxa — elongate, length 39; trochanter segments — 20 and 10; femur — length 60, width 18; tibia — length 87, inner spur 15, outer 10, width of tibia at apex 10; tarsal segments — 30, 15, 10, 7, 10 (pulvillus and pretarsus). Pulvillus terminating in a pointed cone. Claws simple, not surpassing apex of cone.

Wings:—

Fore:—Length 3.6 mm., greatest width 1.3 mm.; infuscated, more deeply so basad of 1st transverse cubitus and recurrent (excepting the lighter area crossing the first cubital cell from parastigma backwards); stigma and venation dark brown; inner side of stigma 25, outer 30, greatest width 0.4 times the length; 1st abscissa of radius 15; 2nd 35; 3rd 70; first intercubitus 30; recurrent 15, portion of cubitus between recurrent and apex of 1st cubital cell 5. Membrane uniformly hairy.

Hind:—Length 2.8 mm.; greatest width 0.7 mm. Infuscated as forewing; first abscissa of mediella 28, second 56; basella 15.

Abdomen:—Oval, greatest width 0.5 times the length; plate of first tergite deeply impressed medially in the anterior portion, the lateral grooves deep, crenulated, the posterior portion of the plate rugoso-punctate; suturiform articulation practically straight, fine and smooth; second and succeeding tergites smooth and shining. Ovipositor sheaths slender, width 5.

Color:—General color castaneous (7-E-10)[5] with the posterior portion of the head, the ocellar plate, the flagella of the antennae, the mesonotum except at notauli and before the pre-scutellar groove darkened through Mandalay (8-L-12) to piceous. Tips of mandibles and pretarsi, excepting the brownish claws, piceous. Ovipositor sheaths piceous. Legs and sides of pronotum copper brown (6-C-12).

[5]Color names from Maerz, A. and M. R. Paul, 1950. A Dictionary of Color. Ed. 2. McGraw-Hill. Numbers within parentheses refer to plate number, column and row.

Holotype in collection of University of Wisconsin. Data on pin "Spooner, Wis. coll. larva VI-24-59. Em. VII-24-1959. I. Millers". "Parasite of *Hylobius radicis* on red pine." The collection date refers to the time when the host larva was collected and the emergence date to the appearance of the adult parasite.

Allotype ♂. Length 3.6 mm. Abdomen 1.8 mm. Very closely resembling the holotype both structurally and in color. Head:—transverse, greatest width 60, depth from vertex to base of mandible 47, length 38; conformation similar to that in holotype except that the space between antennae and ocelli is flattened and the eyes are relatively larger and more protuberant; eye height 29, width 16; malar space 6; temple 16; width of face across lower edges of antennal fossae 32; distance from lower edges of antennal fossae to upper margin of clypeus 13; ocell-ocular line 13; lateral ocellus 6; postocellar line 7; flagellum with 26 segments, the antenna relatively longer than in the ♀, all segments being at least slightly longer than thick. Greatest width of abdomen 60, relatively narrower than that of the holotype; second tergite weakly sculptured over most of its surface.

Allotype in collection of University of Wisconsin. Data same as on holotype.

In addition to the holotype and allotype 13 ♀♀ and 1 ♂ emerged from a single host larva. Within the paratypes the color pattern is constant. In the ♀♀ the number of flagellar segments varies from 22 to 24, the size from 3.4 mm. to 4.0 mm. and the second tergite varies from completely smooth to weakly roughened over all but the apical portion.

Cocoon: The single ovoid cocoon retained is buff in color and measures 4.5 mm. in length and 1.6 mm. in diameter.

A single specimen was also reared from a host larva taken from *Pinus sylvestris* (jack pine) at Danbury, Wis., the host larva being collected VI-30-'59 by Millers and the adult emerging VII-22-'59.

The following notes on the parasite are taken directly from the notes of the junior author.

"P 101.—Collection made at Spooner VI-24-1959 in the hatchery plantation. Pine root collar weevil larva was about three-fourths grown, in a tunnel in bark of living red pine. A small hymenopterous larva was noticed on the body and consequently this larva was placed in a separate bottle. In the laboratory the parasitized larva was placed on filter paper in a metal pill box. The filter paper was kept saturated by a piece of moist cotton. Later more parasitic larvae were observed. These pupated on the filter paper near the cotton. Sixteen adults emerged in 4 to 5 weeks (end of July, beginning of August)."

"P 104.—A parasitized pine root collar weevil larva was collected at Danbury Airport plantation. It was on a jack pine, still growing. Rearing procedure was similar to the above. Adult emerged latter part of July."

(Received March 27, 1960)

A Practical Method for Rearing *Monochamus scutellatus* (Say) and *M. notatus* (Drury) (Coleoptera: Cerambycidae)

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Long-term studies of the biology of bark and cambium-feeding insects have been limited to observations in the field or to rearing methods which present conditions deviating from the natural habitat and requiring considerable labor and material. A simple rearing technique is required which will simulate the normal habitat yet will allow the rearing of a numerous and continuously visible stock of specimens without repeated handling.

Methods used for the rearing of bark- and wood-boring insects are varied. The simplest methods consist of the collection of infested woody material, the caging of such and the capture of adults on emergence. Of necessity the observation of growth, metamorphosis and behaviour of the larvae and pupae cannot be accomplished without a disruption of the habitat. Large containers holding collected larvae and wood or bark are practical with non-cannibalistic larvae and when the bulk production of insects rather than continuous observation is the aim.

For at least temporary observation of the development and activity of larvae small cut branches inserted into glass tubes, and larger branches provided with glass windows have been used. However glass test tubes and Petri dishes, (frequently used for various species of insects,) involve repeated and tedious handling of the insects during the necessary changes of natural or artificial food material. There is often considerable loss of the insect stock either through injuries received or through the introduction of pathogenic organisms. Also, the development and behaviour may be affected by the abnormal habitats in such containers.

A novel and practical rearing method for bark beetle larvae, devised by Bedard (1933) and modified first by Kaston and Riggs (1937) and then by Warren (1958) utilizes cut pieces of bark, containing the larvae, ringed with cotton and mounted between two pieces of glass. The whole set-up is kept moist by dipping it in water. The method permits the observation of the animals during the larval development but it requires the preparation of individual rearing chambers for single specimens, the use of considerable quantities of material, and, if used for large insects, repeated handling for food replacement. The use of the Bedard method with large slabs of pine bark, mounted between two plates of glass, for the rearing of *Monochamus* larvae is not practical because of the difficulties encountered in trying to secure bark of uneven thickness tightly between the panes of glass and because of the tendency of the larvae to escape into the cotton ring or out through it.

Method

A simplification of the glass-bark sandwich method of Bedard was devised on the basis of the observed tendency of *Monochamus* larvae to avoid contact with the external environment, that is: larvae when confined in a piece of pine bark between two panes of glass mine throughout the thickness of the bark and often disappear from sight, but larvae in bark with only one pane of glass against the inner bark surface, instead of escaping through the uncovered side of the bark, remain next to the glass. As the firm mounting of a piece of uneven bark against a single glass pane was not successful, a glass substitute was needed which could bend with but which would not deeply impregnate the bark or prove toxic to the animals. A 25 per cent solution of "Vinylite" resin (available from the Car-

bide and Carbon Chemicals Corp., 30 E. 42nd St., N.Y.) in acetone, when applied to the surface of the inner bark of pine or to any wood surface tested, did not penetrate the wood tissues deeply, yet formed a firm and transparent film, adhering satisfactorily and bending with the bark during changes in the moisture content of the wood. The strength of adhesion between the plastic film and wood or bark could be lessened by slightly wetting the latter surface, waiting until all visible moisture was absorbed, and then applying the plastic coating. Such a wetting also facilitated the burrowing activities of implanted borer larvae.

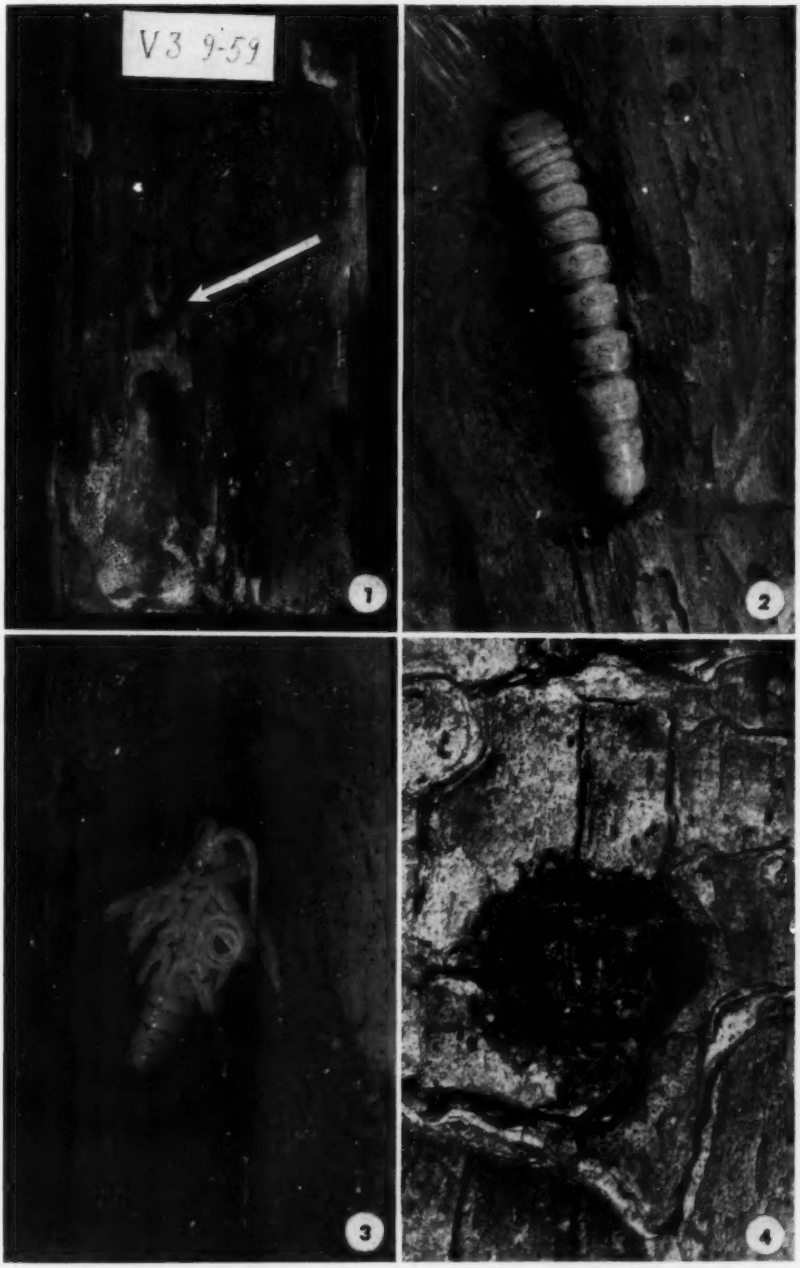
The rearing chambers were prepared in the spring by peeling the bark, together with a cambium layer, from white pine cut during the preceding winter and not yet infested with insects. The bark chosen came from large trees and had a thickness estimated to be sufficient for accommodating the largest mature *Monochamus* larva. The bark was sawn into rectangular slabs, approximately 6 x 12 inches in size, which were stacked outdoors to dry until they lost their flexibility. Excessive curling was prevented by weighting the stacks.

With a large brush the "Vinylite" solution was quickly applied to the inner surface of the bark, taking care to carry the coating over onto the rough cut edges of the slabs, thereby ensuring an excellent adhesion of the film. After about two hours of drying a second plastic coat was painted on the bark, avoiding excessively liberal application which could lead to bubble formation during drying. The rearing chambers were dried until no odor of acetone was detectable, a process lasting for about two days at room temperature.

The animals reared were the larvae of *Monochamus scutellatus* and *M. notatus*, collected as larvae of the first instar or obtained as eggs deposited on the slabs of bark. With the collected larvae one animal was implanted in each chamber through a hole, approximately 3 inches deep, drilled from the edge of the slab to just under the vinyl film. The drill hole was made wide enough for the larvae to turn around in freely. The holes were tightly plugged with cotton. From this hole the larva started its own mining. The larvae which hatched from *Monochamus* eggs voluntarily bored through the entire bark and appeared in the cambium-plastic interface. The rearing chambers, hanging on wire hooks supported by a horizontal rod, were suspended in large battery-jars above a one per cent aqueous solution of sodium propionate. The propionate solution prevented a profuse development of molds on the frass expelled from the chambers. The jars were loosely covered with sheets of polyethylene. This maintained a humid atmosphere around the bark. Care was taken to prevent close contact between the bark slabs, thereby eliminating attempts by the larvae to move from one slab to another. Rearing was effected at uncontrolled room temperature. The overwintering took place in an unheated room at near freezing temperatures.

Owing to the discontinuation of our experiments with *Monochamus* larvae soon after the rearing experiment was started, only 15 rearing chambers were prepared and maintained. Each contained one larva and was observed until the emergence of the adult beetle. Of the 14 beetles reared 10 were identified as *Monochamus scutellatus* and 4 as *M. notatus*. One specimen died, apparently as a result of an incomplete ecdysis.

Since all the larvae mined in the inner bark next to the plastic surface, an unobstructed view of them during the entire cycle of development was afforded. Measurements of their size as well as detailed observations of their behaviour were possible. Figures 1-4 show photographs of animals in their bark slabs. In spite of the formation of some cracks in the vinyl film none of the larvae attempted to escape from the rearing chamber as long as the bark or plastic did not touch any other surface. The cracks were used by the larvae for the disposal of frass.



Figs. 1-4. 1, Bark-vinyl rearing chamber with larva; 2, Larva and its mine in the bark; 3, Pupa in its pupal chamber; 4, Adult *Monochamus scutellatus* making its exit.

Figs. 2 and 3 were photographed through the "Vinylite" coating.

Overwintering and pupation took place within pupal chambers constructed in the bark yet visible to the observer through the plastic window. The adults with the exception of three specimens left the pupal chambers by chewing their way through the remaining thickness of outer bark, not through the plastic. Only at the initial setting up of the rearing chambers were the insects handled. The food supply available in the pine bark slabs proved to be more than adequate for the development of the larvae. The only attention given to the rearing set-ups, other than observation, was the occasional replenishment of the water in the bottom of the large jars.

Discussion

The vinyl-coated bark slabs so closely resembled a completely natural habitat that the behaviour of the woodborers apparently deviated from that in undisturbed trees only in one respect: the pupal chambers were constructed in the bark instead of in solid wood. As evidence of the normalcy of the habitat in the slabs is the fact that the larval mines were always in the inner bark and in contact with the vinyl films, also the insects did not attempt to escape through the film even when they became adult. With other types of rearing chambers constant effort to escape with considerable success was noted. In addition to the excellent opportunity to observe the animals in the chambers the technique provides a simple means for bulk rearing of *Monochamus* with minimal time and labor requirements and at a negligible cost of materials. It also affords virtually complete freedom from mortality caused by repeated handling and by introduction of pathogens. The method is likely to be applicable to other cambium-boring insect larvae with the exception of those species which mine into the bark and would not confine themselves close to the transparent plastic layer.

Summary

The observed tendency of *Monochamus* larvae to avoid contact with extracortical environment was successfully utilized to make rearing chambers of natural white pine bark in which the implanted larvae were isolated, on one side, by the normal thickness of the bark and, on the other side, by a transparent coating of vinyl plastic, replacing the sapwood.

Pieces of whole white pine bark were used to construct the chambers, 6 x 12 inches in size, and coated twice on the inner surface with a 25 per cent solution of "Vinylite" in acetone. One larvae was introduced into each slab of coated bark. These were suspended over water in glass jars and required no subsequent handling until the completion of the life cycle of the animals.

The *Monochamus* larvae mined in the inner bark layers, next to the plastic film only, never becoming obscured from view, constructed their pupal chambers in the bark, and finally in most instances emerged through the outer bark.

Acknowledgment

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Unusual Occurrence of the Virginia Pitch-Nodule Moth, *Petrova wenzeli* (Kearfott), in Canada (Lepidoptera: Olethreutidae)

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Recent study of three Ontario *Petrova* specimens in the Canadian National Collection, tentatively identified as *P. albicapitana* (Busck), showed them to be the Virginia pitch-nodule moth, *P. wenzeli* (Kearfott). This insect was previously unknown outside the range of its Virginia pine host, *Pinus virginiana* Mill. (Miller and Altmann, 1958). Following this discovery, the Canadian Forest Insect Survey assembled nearly 300 specimens labeled as *Petrova albicapitana* for restudy, and among these 2 more *P. wenzeli* specimens were identified by the writer. With the writer's differentiation guide given below, Forest Insect Survey personnel distinguished two more *P. wenzeli* moths from a large group of *P. albicapitana* specimens reared subsequently.

Taxonomically and ecologically *P. wenzeli* is similar to *P. albicapitana.* Both species have two-year life cycles, and both develop in blister-like pitch nodules on twigs and branches of pine. Adults can be readily separated with two sets of color characters: color of underside of forewing and both sides of hindwing—gray in *P. albicapitana,* light brown in *P. wenzeli*; forewing markings—black subterminal line and black scales scattered throughout in *P. albicapitana,* rust subterminal line with black scales absent in *P. wenzeli.* Genitalia of either sex of both species are indistinguishable.

To date, *P. wenzeli* records for Canada—all from Ontario—can be summarized as follows: four moths from Merivale, near Ottawa, reared in 1949 and 1950; one moth from Presquile, near Owen Sound (1951); one from Normandale, near Long Point (1959); and one from Ridgeway, near Port Colborne (1959). The host of all seven specimens was jack pine, *Pinus banksiana* Lamb. Except for Presquile, where only one insect was collected, these localities produced much larger numbers of *Petrova albicapitana* adults which suggests that *P. wenzeli* individuals were scattered here and there among *P. albicapitana* populations. The *P. wenzeli* specimens represent about 3 percent of the number of *P. albicapitana* moths reared by the Forest Insect Survey in Ontario.

The Canadian locality records are from 100 to 250 miles distant from the range limit of Virginia pine (as given by Little, 1949). The explanation for these occurrences of *P. wenzeli* can only be guessed. Before they came to light, Miller and Altmann (1958) had postulated that dispersal of these moths by convective transport across the *Pinus virginiana-Pinus banksiana* gap might be taking place.

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Book Review

Dragonflies, by Philip S. Corbet, Cynthia Longfield, and N. W. Moore, The New Naturalist Series, No. 41, pp. xii + 260, 53 coloured plates, 16 half-tones, and 200 maps and diagrams. Collins, London, England. Price 42s.

This admirable book deals with the systematics and biology of the British Odonata, but its usefulness will extend far beyond the limited geographical scope of its subject matter. Very full specific information is given on the characteristics, distribution and habits of the 43 British kinds of dragonflies and damselflies, but the general picture is never lost from view. The authors on the one hand do not shrink from discussion of recondite features of development, behaviour, distribution and ecology; on the other hand they are not too academic to discuss in clear and informative detail such practical matters as preservation of specimens and marking of living individuals. The easy and lucid style is in the excellent tradition of the better British scientific writing. The illustrations match the text in value. Fine morphological drawings of nymphs and wing-venation are supplemented by most interesting sketches depicting aspects of development and behaviour. Not only the British distributions, but also the total ranges, of representative species are shown; the latter are presented in very appropriate North-polar and oblique projections. Good black-and-white photographs of habitats and life-stages are provided, but special mention must be made of the really superb coloured photographs made from life by Mr. Sam Beaufoy that illustrate the majority of species. I defy any entomologist to read this book without having his interest in dragonflies quickened and his appetite for biological study whetted.

EUGENE MUNROE

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